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Inactive Sulfide Mounds of the Manus Basin: Invertebrate Composition and Potential for a Chemoautotrophic Food Web

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ABSTRACT PAGE

Inactive sulfide mounds are commonly observed along mid-ocean ridges and back-arc basins. These areas of inactivity support dense communities of macro- and megafaunal invertebrates yet; the invertebrate composition has not been deliberately studied. Biological sampling of representative macro- and megafauna was carried out in the Suzette vent field, Manus Basin (~1500 m) to characterize the invertebrate community that colonizes the inactive sulfide mounds and active vent chimneys, and to use stable isotope analyses to investigate the source of primary production. We address these topics specifically because inactive hydrothermal systems, specifically in back-arc basins, have become of particular interest to mining companies due to deposits of commercially valuable ores. Test mining is already underway in the Suzette vent field and although the focus is on inactive sulfide mounds (their close proximity to active hydrothermal vent habitats will likely be affected). Characterization of the invertebrate communities show faunal differences between inactive and active habitats and hace helped anticipate the impacts of mining at inactive and peripheral active habitats. Stable isotope analyses (δ13C, δ15N, δ34S) indicate that invertebrates at active hydrothermal vents consume chemosynthetic sources with some evidence of a mixed photosynthetic diet. Accumulation of photosynthetically derived POM may become enhanced at active vent sites due to topography relief and/or thermal convection cells. Carbon stable isotope analyses of invertebrates from inactive sulfide mounds show values indicating a possible mixed diet of two isotopically extreme sources. Nitrogen and sulfur stable isotope compositions at inactive sulfide mounds suggest a chemosynthetic source that is either advected from near by active vent plumes or is possibily in situ microbial production of organic carbon. Overall, there is some contribution of chemosynthetic primary production at inactive sulfide mounds and we infered that this contribution is due to chemoautotrophic bacteria mobilizing particulate metal sulfides from inactive sulfide mounds.

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INTRODUCTION

Invertebrate communities associated with active deep-sea hydrothermal vents have been the focus of considerable research since the first report of the Galapagos hot springs in 1977. Active hydrothermal vents are ephemeral, extreme environments colonized by endemic invertebrate taxa (Corliss et al. 1981). Hydrothermal vent formation begins as natural seawater seeps below the ocean seafloor and becomes super-heated (Van Dover 2000, Halfar & Fujita 2001). The percolating water reacts with the surrounding rocks, leaching metals and eventually building up enough thermal buoyancy to rise and mix with cold, oxygen-rich water. As the extreme temperatures mix, dissolved metals precipitate, forming sulfide chimneys (i.e., polymetallic sulfide deposits; Haymon 1983). These polymetallic sulfide deposits continue to build, providing more and more substrate for a variety of invertebrates and metabolically diverse microbes that sustain life in these environments (Corliss et al. 1981, Van Dover et al. 1990).

In time, hydrothermal activity terminates and sulfide chimneys topple, leaving piles of metal-rich mounds on the seafloor and an environment that no longer delivers the fluid flux that is required by endemic vent organisms. The absence of noxious concentrations of dissolved hydrogen sulfide and warm fluid flux, in turn, provides a hospitable new environment to a different suite of megafaunal species. Explorers of active vents often encounter sulfide deposits that are remnants of former activity. Despite the fact that some of these old sulfide mounds are colonized by an unusually high biomass of invertebrates, little is known about the taxonomic composition of this

community and how it is sustained. Photographs were taken from Gorda Ridge during 1988 field programs using *Alvin* and *Sea-Cliff* deep-diving submersible (Van Dover et al. 1990), the Fiji/Lau Basins during the 2005 research cruise using remote-operating vehicle (ROV) *Jason II*, and most recently the 2006 Manus Basin research cruise using the *TST212* ROV. Photographs often document dense patches of suspension-feeding macro- and megafaunal invertebrates colonizing the inactive sulfide mounds. Suspension-feeders were considered to be non-vent species consisting mainly of large assemblages of branching corals, stalked barnacles, hydroids, solitary tunicates, brisingid seastars, crinoids, carnivorous sponges, anemones and brachiopods (K. Erickson pers. obs., Van Dover et al. 1990). While it is routine to observe megafauna and macrofauna associated with inactive sulfide mounds along mid-ocean ridges and spreading centers of back-arc basins, there is little is known about the role of microbial primary production (based on oxidation of mineral sulfides) in the nutrition of the invertebrates.

At least 3 non-exclusive conditions could provide nutritional options:

1) low-level venting of hydrothermal fluids could actually be continued at these "inactive" sites, supporting chemoautotrophic production within the overlying water column;

2) *in situ* production of organic carbon from acid-labile sulfides mobilized by microbial activity to support primary production (chemoautotrophic);

3) topographic relief may change the local flow regime of the mounds, concentrating suspended particulates for the biota to feed upon (either

chemosynthetic from nearby active sites, or photosynthetic, from sinking particles).

It is feasible that microbial oxidation of mineral (particulate) sulfides can provide enough energy for the growth of chemoautotrophic microorganisms (Edwards K 2000, Edwards et al. 2003, Suzuki et al. 2004). Oxidation of polymetallic sulfide minerals by chemooautotrophic bacteria has been reported (Eberhard et al. 1995), raising the possibility that mineral sulfides themselves (not just dissolved sulfide from vent fluids) can serve as chemical resources for primary production by microbes, nutrients from which might in turn be transferred through a food web.

Chemoautotrophic bacteria form the base of the localized active hydrothermal-vent food web (Karl 1995). These microbes fill their ecological role in the vent community either as free-living bacteria (suspended in the water column and/or growing on surfaces), or as endo and episymbionts of invertebrate hosts. Primary consumers tend to consist of grazers, suspension feeders, and deposit feeders, as well as the invertebrate hosts of endosymbiotic, autotrophic bacteria (Galkin 1997). Secondary consumers in the hydrothermal vent system can include carnivorous fish (Zoarcidae gen sp.), predatory snails (*Eosipho desbruyeresi*; Okutani & Ohta 1993), as well as opportunistic squat lobsters (*Munidopsis* spp.) and crabs (*Austinograea alaysae*; Galkin 1997). These are the generalized schemes of trophic interactions observed in hydrothermal-vent ecosystems (Tunnicliffe 1991); however regional differences are observed due to species composition of the community. For example, mussels of the genus *Bathymodiolus* which host endosymbionts, and the

shrimp, *Rimicaris exoculata,* host episymbionts are abundant at active vents along the Mid-Atlantic Ridge (Van Dover et al. 1988, Desbruyeres et al. 2006). At vents on the East Pacific Rise, biomass is dominated by vestimentiferan tube worms (*Riftia pachyptila*), and at the Central Indian Ridge, vents are dominated by endosymbiont-hosting gastropod species (*Alviniconcha* sp., *Ifremeria nautilei*), mussels (*Bathymodiolus* sp.), and episymbiont-bearing shrimp (*Rimicaris* cf. *exoculata).* While primary production is dominated by chemoautotrophic endo- and epi-symbiotic bacteria, there are multiple sources of organic material that could be used as alternative resources. For example, free-living, and mat-forming chemoautotrophic bacteria growing on surfaces (e.g., rocks, shells) serve as a source of nutrition for grazers and deposit feeders (Van Dover & Fry 1994, Galkin 1997, Windoffer & Giere 1997). Photosynthetically-derived organic particles rain down into these active vent systems and provide another source of energy for vent organisms (Van Dover & Fry 1994, Galkin 1997).

Stable isotope techniques have been used extensively in the study of food web energetics (Peterson & Fry 1987, Conway et al. 1989, Fisher 1990, Kennicutt et al. 1992), especially in extreme environments where traditional food web methods are generally not practical in terms of feasibility and effectiveness. Stable isotope analysis ($\delta^{12}C$, $\delta^{15}N$, $\delta^{34}S$) provides a continuous measure of trophic position that integrates the assimilation of energy to the different trophic pathways (Conway et al. 1989), allowing ecologists to identify and quantify trophic pathways through interpretation of diet over long-time scales.

Carbon stable isotope composition shows fidelity between diet and consumer (trophic shift ~ 1 ‰ ; Peterson & Fry 1987), while sulfur stable isotope composition further emphasizes the autochthonous nature of food webs and is a useful discriminator of nutritional modes (Fry et al. 1983, Van Dover & Fry 1989, Vetter & Fry 1998). Nitrogen stable isotope composition provides information regarding trophic complexities via a stepwise enrichment (~3.5 ‰) from diet to consumer (Minawaga & Wada 1984, Van Dover & Fry 1989). However, there remain gaps and uncertainties in our understanding of isotopic systematics around active hydrothermal vents. The composition of carbon stable isotopes reflect these anomalies and does not always accurately indicate trophic level (Macko et al. 1982, Rau et al. 1983, Focken & Becker 1998). Multiple sources of particulate organic matter (POM) entering a system are believed to produce intermediate carbon isotope values (Van Dover & Fry 1994, Van Dover 2002). Such ambiguous values can indicate a mixed diet of two isotopically extreme sources (Fry B. 1984, Van Dover & Fry 1994, Van Dover 2002). Examples of these ambiguous values are observed at active hydrothermal vents, where photosynthetic debris is rained into the a chemosynthetic based system (Tunnicliffe 1991, Van Dover & Fry 1994, Galkin 1997, Van Dover 2002), and possibly at inactive sulfide mounds where active venting occurs within close proximity.

Variability in nitrogen concentration and isotopic composition in sediment make it difficult to interpret nitrogen isotope values due to processes such as diagenesis, remineralization/degradation and even size class of POM (Cifuentes et al.

1988, McCutchan Jr. et al. 2003). Recently, sulfur composition has increased in popularity as an additional tracer where isotopic signatures of two producers are not separated using carbon and nitrogen (Connolly et al. 2004). Sulfur isotopic values appear to have fewer inconsistencies than carbon and nitrogen due to characteristics specific to sulfur isotopes (Connolly et al. 2004). Ratios between the "heavy" and "light" sulfur isotopes have large differences between sources used by consumers making isotopic differences amongst producers more likely to be a function of source rather than that of metabolic fractionation (Fry et al. 1983, Peterson & Fry 1987, Conway et al. 1994, Vetter & Fry 1998).

Knowledge of taxonomic communities at inactive sulfide mounds and what sustains them is becoming increasingly important since deep-sea mining has become a reality in regions of back-arc spreading (Gaylord 2000, Wiltshire 2000b, Shipboard Scientific Party 2001). Land-based sulfide deposits that contain economical concentrations of gold and copper were originally formed on the seafloor (Simpson 2006). Giant land-based deposits of lead and zinc (excess of 100 million tonnes) were originally formed in a marine hydrothermal environment (Gaylord 2000). Hence, hydrothermal vent habitats or more specifically, inactive polymetallic sulfide mounds have become the targets of deep-sea mining. Mining interests of inactive polymetallic sulfide mounds have not only increased due to the discovery of massive deposits of commercially valuable ore, but have also increased due to 1) advances in remote sensing, positioning and underwater technologies (Wiltshire 2000a); 2) discovery of gold and silver deposits in relatively shallow water (Iizasa 1999, Glasby

2000, Wiltshire 2000a); and 3) prospecting activities within the EEZs (Environmental Economic Zones) of several countries (i.e. Papua New Guinea and Fiji; Halfar & Fujita 2001).

Deep-sea mining may be more cost-effective that terrestrial mining. Unlike submarine ploymetallic sulfide deposits, land-based mineral deposits are not as easily detected because they are typically deep underground and may be thousands of kilometers away from where they were formed millions of years ago (Simpson 2006). Plume detection from submarine hydrothermal vents, however, is relatively easy and, as there are numerous active hydrothermal vent systems discovered on the sea floor worldwide, there is potential for many more extinct or inactive hydrothermal fields in the surrounding areas (Simpson 2006). If high-grade resources are found in the deep sea, capital and operating costs of mining are thought to be much lower compared to land-based operations for many reasons:

1) No costly mining shaft is sunk; rather a pipe deployed through the water

2) No overburden needs to be removed as in an open cut mine

3) Seafloor is soft, so there is no need for a drill blast excavation

4) Ability to float and redeploy infrastructure from site to site, reducing capital

5) Minerals do not cover habitable land; meaning there are no access rights (Simpson 2006).

In 1991, inactive polymetallic sulfide deposits of the Manus Basin, Papua New Guinea (Figure 1) were found to contain metal grades as high as 13% copper, 47% zinc, 22 grams gold/tonne and 327 grams silver/tonne, which are believed to be

comparable to the best terrestrial deposits ever discovered (Simpson 2006). Manus Basin is surrounded by the islands of Manus, Papua New Guinea (PNG), New Britain and New Ireland and is located just north of Woodlark Basin and behind the New-Britain arc-trench system (Figure 1). In 1997, Nautilus Minerals was granted two exploration licenses covering the seafloor deposits off the coast of PNG. Test mining off the coast of PNG began in January 2006, and mining operations are expected to begin within 5-7 years of the test mining (Broad 1997, Gaylord 2000, Wiltshire 2000a).

Mining of polymetallic sulfide deposits will impact inactive hydrothermal vent environments and depending on the proximity, active hydrothermal vents as well. Deep-seabed mining is analogous to strip mining of terrestrial environments (Jumars 1981). Localized and possibly extensive destruction from mining of inactive sulfide mounds will be observed. Removal of inactive sulfide mounds is removal of much of the hard substrate present in these areas, disturbance of surface and subsurface seafloor, and disturbance of surrounding areas due to resuspension of surface and subsurface sediments. (Jumars 1981, Smith & Kauffman 1999, Glover & Smith 2003). Given the lack of information available (i.e. taxonomy, species structure, biogeography, basic natural history) concerning inactive sulfide mounds, it is possible that these biologically important ecosystems could be altered or destroyed before fundamental research is completed. In this study, we identify mega- and macro-invertebrate species that colonize inactive sulfide mounds and report the results of stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) regarding microbial primary

production and the possible contributions to different trophic pathways in the Suzette vent field.

METHODS

Overview of Sampling Effort

This study is the outcome of the research cruise to the Manus Basin, Suzette hydrothermal vent field (Figure 2) undertaken by the M/V *DP Hunter* from Dec. 31, 2005 to January 30, 2006. Animals were collected from 5 active sample locations (Kowalczyk, Binns, Williamson, Fullagar Extended) and 9 inactive sample locations (Kowalczyk, Binns, Williamson (3 samples), Fullagar Extended, Nat Nat, 99, Paine) within the Suzette hydrothermal vent field (3°47.45'S, 152°5.65'E, 1520 m; ~ .81 km^2; Figure 3; Table 1) in the Manus Basin using the remote operated vehicle (ROV) *TST212* on board the *M/V DP Hunter*. Sample locations were chosen based on real time digital video observations made during transects. Locations within the Suzette vent field that were observed to have a high biomass of invertebrate taxa on inactive sulfide mounds were chosen for inactive invertebrate sampling and areas observed to have a high biomass of vent endemic taxa on active sulfide chimneys were chosen for active invertebrate sampling (Table 1). Typically site locations (e.g., Williamson, Binns, Fullagar Extended, Kowalczyk) were comprised of both active hydrothermal habitats, as well as inactive habitats (non-venting remnant chimneys), providing the opportunity for sampling of both habitats of interest.

Sampling methods

Specimens were collected using a suction sampler, biological scoop, or ROV claw and five-function manipulator; voucher specimens are retained in archival collections at the Duke University Marine Laboratory (Beaufort, NC). Invertebrate specimens were preserved for laboratory identification and collection in a 10% formalin solution for 24 hours then transferred to a 70% EtOH buffered solution. Specimens were later identified in the lab and experts were consulted for verification and confirmations of taxonomic identifications. Samples of animal tissue were also collected for stable isotope analyses and phylogenetics. The stable isotope samples were dried and ground in to a fine homogeneous powder, placed into tin capsules, and taken back to the lab for further analysis (see *Stable Isotope Analysis*). A total of 34 individual invertebrates (5 *Alviniconcha* sp., 1 *Ifremeria* sp., 5 *Chorocaris* sp., 19 *Eochionelasmus* sp., 4 *Lepetodrilus* sp.) were collected for DNA analysis. Muscle tissues samples from each individual were collected and preserved on Whatman FTA cards (see *Phylogenetic Analysis*).

Taxonomy

Voucher specimens were collected and used to identify invertebrates to lowest taxonomic level (Table 2). Once organisms were identified in the lab, specialists were consulted to verify specific identities: hydroids, Dr. Dale Calder, Department of Natural History, Royal Ontario Museum; ophiuroids, Dr. Sabine Stöhr, Swedish Museum of Natural History; gastropods, Dr. Anders Waren, Swedish Museum of

Natural History; shrimp, Dr. Michel Segonzac, Ifremer; anemones, Dr. Daphne Fautin and Andrea Crowther, Natural History Museum and Biodiversity Research Center, University of Kansas; polychaetes, Jennifer Dryer, Virginia Institute of Marine Science; barnacles, Dr. William Newman, Scripps Institute of Oceanography; carnivorous sponges, Dr. Jean Vacelet, Centre d'Oceanologie de Marseille; corals, Dr. Phil Alderslade, Museum and Art Gallery of the Northern Territory, Australia.

Phylogenetic analysis

Molecular analyses were conducted at the Monterey Bay Aquarium Research Institute with the help of Dr. Robert Vrijenhoek, Shannon Johnson, and Dr. Joe Jones. 16SAR/BR was used for PCR amplifications of 568 bp of the 16S rRNA gene (Palumbi 1992), as well as COIF_1777 (TAATGTAATTGTAACAGCTCATGC) and HCO_2198 (Folmer et al. 1994). Whatman FTA cards were used to preserve tissue. Tissue was cut from an organism and placed onto FTA card and squished into FTA paper with top portion of FTA card with finger and thumb. Five individual *Alviniconcha* sp., one individual *Ifremeria* sp., nineteen individual *Eochionelasmus* sp., five individual *Chorocaris* sp., and four individual *Lepetodrilus* sp. samples were stored at room temperature until they could be processed at the lab. Standard Whatman FTA card punch was used to extract 1 mm discs to be used in PCR. Each punched disc it was placed in a 200 µl, 1% SDS, 2mmEDTA pH 8.0 for 10 minutes. SDS was then washed out with 200 ul of TE buffer, allowing a five minute soak time. This wash was repeated 3 times, after which the TE buffer was rinsed off with 200 µl

of 100% isopropanol and centrifuged for 5 minutes at 55 degrees. The 1 mm punch disc was then placed in PCR.

PCR was conducted in a 25µl solution that included 30–100 ng of template DNA, 2.5 µl of 1x of PCR buffer (supplied by manufacturer), 2.5 µl of 2.5µM $MgCl_2$, 1 µl of each primer (10 µM final conc.), 2.5 units *Taq* polymerase (Promega Biosciences Inc., San Luis Obispo, CA), 2.5 µl of 2mM stock solution of dNTPs, and sterile water to final volume. Amplifications for *COI*, which occurred with a Cetus 9600™ DNA Thermal Cycler (Perkin-Elmer Corp. CT), used an initial denaturation of 95°C / 5 min, followed by 35 cycles of 94°C /1 min, 55°C / 1 min, and 72°C / 2 min, and a final extension at 72°C / 7 min. Amplifications occurred with a DNA Engine (PTC-200) Peltier Thermal Cycler (MJ Research, Inc., Waltham, MA), used an initial denaturation of 95°C / 5 min followed by 35 cycles at 94°C / 1 min, 54°C / 1 min, and 72°C/ 2 min, and a final extension at 72°C/ 7 min. PCR products were purified by gel excision and cleaned with Montage filter units (Millipore Corp. Billerica, MA). PCR products were sequenced bidirectionally with the same primers used in PCR on an ABI 3100 capillary sequencer using BigDye terminator chemistry (Applied Biosystems Inc., Foster, CA). DNA sequences were proofread using Sequencher v 4.1 (Gene Codes Corp. Inc., Ann Arbor, Michigan) and aligned using Clustal X (Thompson et al. 1994) and by eye. After sequencing, data were exported as aligned nexus files from sequencher. Additional sequences from GenBank were incorporated into the dataset at this point.

Video analysis

In situ observations of invertebrate macro and megafauna distributions and habitat observations of gradients were documented by digital video and digital photographs, recorded during periods of exploration and sampling of biological communities at the Suzette hydrothermal vent field (>75hrs) using the ROV *TST212*. Video, photographs, and detailed logs are also archived at the Duke University Marine Lab. Maps of hydrothermal activity, inactivity and bathymetry were generated from data generated through transponder navigation, side scan multibean sonar and real-time video analysis/logging during ROV transects.

Stable isotope analysis

Stable isotope analyses (^{13}C, ^{15}N, or ^{34}S) were conducted by Dr. Stephen Macko (Environmental Sciences Laboratory, University of Virginia, Charlottesville). Animal tissue samples and sediments were acidified to remove carbonate. Muscle tissue was utilized for large specimens while smaller organisms were ground up whole and sometimes pooled with like species when unable to identify to species (i.e., limpets, isopods, amphipods and hydroids). Carbonate-free residues were weighed into tin capsules and converted to CO_2, N_2 and SO_2 for isotope analysis using a Carlo Erba elemental analyzer coupled to an OPTIMA stable-isotope-ratio mass spectrometer (Micromass, Manchester, UK). The outer surface of sulfide rock was analyzed for organic sulfur stable isotopes but not carbon or nitrogen isotopes. Carbon and nitrogen isotopic ratios were determined with a single combustion using a

dual furnace system composed of an oxidation furnace at 1020°C and a reduction furnace at 650°C. Using the Carlo Erba elemental analyzer, samples for sulfur were separately pyrolyzed at 1050°C by means of a combination oxidation and reduction furnace system. The resulting gases were chemically dried and directly injected into the source of the mass spectrometer. Isotopic composition of stable isotopes is expressed as a ratio (R) between two isotopes

$$R = {}^{n}X:{}^{n}X$$

The standardization of *R* is express as a delta value (δ):

$$\delta^{n}X = (R_{sample} / R_{standard} - 1) * 1000\ ‰ \text{ (parts per thousand or per mil),}$$

where *X* is the heavy isotope (^{13}C, ^{15}N, or ^{34}S), *R* is the abundance ratio of the heavy to light isotopes ($^{13}C/^{12}C$, $^{15}N/^{14}N$, or $^{34}S/^{32}S$). Standard reference materials assigned $\delta^{n}X$ values of 0.0 ‰ are the fossil of *Belemnita americana* from the PeeDee formation in South Carolina for carbon, atmospheric air for nitrogen, and the Canyon Diablo meteorite for sulfur. In practice, samples are measured against tanks of carbon dioxide, nitrogen, and sulfur dioxide gases that have been calibrated against NBS 22, atmospheric N_2 and NBS 127, respectively. For sulfur and carbon, the value is corrected for mass overlap with the isotopes of oxygen. Reproducibility of the measurement is typically better than ±0.2‰ for these elements using the continuous flow interface on the OPTIMA.

RESULTS

Study Sites

The Suzette vent field lies within Manus Basin, approximately 60 km northwest of Rabaul, on the East New Britain Province of Papua New Guinea (Figure 2). The crest of the Suzette vent field is at ~1460 m and is characterized by forests of hundreds of active and inactive massive sulfide chimneys. Active chimneys and inactive sulfide mounds were seen in all shapes and sizes: from small deposits with < 0.5 m relief above the seafloor, to slender, finger-like sulfide branches reaching >10 m above the seafloor, to extensive fields of chimneys with diameters of 3 m or more. The Suzette vent field was dominated by inactive chimneys (~75% coverage) and clear diffusing vents (~25%). Black smokers (116°C – 296°C), grey smokers and white smokers (95°C-119°C) were interspersed throughout the Suzette field. In most areas where active hydrothermal venting was observed, there were also remnants of old sulfide chimneys (no longer actively venting), so we were able to collect both inactive and active invertebrates within the same site.

Submersible observations of the faunal setting

Invertebrates from 5 phyla (Cnidaria, Porifera, Annelida, Arthropoda, Echinodermata) were represented at inactive vent sites (Table 2). Invertebrates representative of 23 species were collected at inactive sulfide mounds. Invertebrates observed and collected at inactive sulfide mounds were non-vent endemic species and were dominated by either large assemblages of branching bamboo coral (*Keratoisis*

sp.) or stalked barnacles (*Vulcanolepas* cf. *parensis*, *Neolepas* cf. *zevinae*). Numerically dominant organisms found within inactive areas consisted of hydroids and a cladorhizid carnivorous sponge (*Abyssocladia dominalba*). Occasional sightings of ophiuoroids (*Ophiacantha* sp., *Ophiura* sp.), a deep-sea holothurian (*Enypneastes* cf. *exemia*), and anemones (cf. *Hadalanthus* sp.) were also recorded (Table 2). Zoarcid fish were observed throughout the inactive and active areas within the Suzette vent field. Galatheid squat lobsters (*Munidopsis lauensis* and *M. starmer*), shrimp (*Chorocaris vandoverae*), and stalked barnacles (*Vulcanolepas cf. parensis*) were observed at inactive and active sulfide mounds.

Invertebrates from 4 phyla (Cnidaria, Annelida, Mollusca, Arthropoda) were represented at active vent sites (Table 2). Invertebrates representing 31 species were collected at active vent sites (Table 2). Manus Basin is known to have *Alviniconcha* sp.1 but not *Alviniconcha hessleri* or *Alviniconcha* sp.2 (Kojima et al. 2001a). This was supported by DNA samples taken from the Suzette vent field, Manus Basin as they resulted in only *Alviniconcha* sp. 1 being reported. *Ifremeria nautilei* and *Alviniconcha* sp.1 were the overwhelming biomass dominant organisms at active hydrothermal vent chimneys in the Suzette field. These provannid gastropods were typically found in large sedentary aggregations (>100 individuals) within the shimmery water zone of the active vent. *Ifremeria nautilei* was observed to typically outnumber *Alviniconcha* sp.1. One other gastropod species in the family Buccinidae (*Eosipho desbruyeresi*) was also observed and collected within the Suzette field. This species was commonly seen crawling on thick barnacle-encrusted chimneys but this

species was solitary and not observed to be nearly as abundant as the provannid gastropods.

Sessile barnacles (*Eochionelasmus ohtai* cf. *manuensis*) were a numerically dominant organisms sampled from active vent sites; they occurred as massive aggregations encrusting sulfide chimneys. Pyropeltid (*Lepetodrilus schrolli*) and Phenacolepadid limpets (*Olgasolaris tollmanni* and *Shinkailepas tufari*) were also observed and collected in abundance from the shells of the provannid gastropods (*Alviniconcha* sp.1 and *Ifremeria nautilei*). The taxonomy of *Lepetodrilus schrolli* has been confusing. It has been reported from the Marianas Trench, near Japan, and in Lau and Fiji Basins, as well as in Manus Basin. Specimens of this morphotype from the Suzette vent field, Manus Basin are morphologically (A. Waren, pers. comm.) and genetically (this study) different from "*L. schrolli*" identified from the Mariana Trough, Fiji and Lau Basin, indicating that the Mariana Trough and the Fiji/Lau Basin limpets are each new species.

Polynoid (scaleworms), alvinellid, and ampharetid polychaetes were also numerically dominant groups sampled at active Suzette vent chimneys. Crustaceans at the active chimney sites included alvinocarid shrimp (*Chorocaris vandoverae*), bythograeid crabs (*Austinograea alayseae)*, and galatheid squat lobsters (*Munidopsis lauensis and M. starmer*). Molecular sequences of barnacles (*E. ohtai* cf. *manuensis*), bythograeid crabs (*Austinograea alayseae*), and shrimp (*Chorocaris vandoverae*) were obtained, but the lack of sequence data for related taxa in GenBank makes it

impossible to determine the relationship of these specimens to representatives from other back-arc basins or elsewhere.

Brief descriptions of inactive sample locations

There were 9 inactive sample locations. Of the inactive sites, Williamson and 99 showed the largest areas of inactive sulfide mounds and supported the highest biomass and abundance of deep-sea, non-vent-endemic taxa. Fullagar Extended, Kowalczyk, Binns, and Kowalczyk (active venting and inactive sulfide mounds observed) were mainly comprised of active venting interspersed with inactive sulfide mounds. The inactive sulfide mounds were abundant and supported a high abundance of the numerically dominant biomass. Paine, 99, and Nat Nat had large areas of typical deep seafloor with more specific areas of inactive sulfide locations.

Kowalczyk

This location was characterized by extensive forests of active chimneys and inactive sulfide mounds. Tall inactive sulfide mounds were continuous with active chimneys, making specific habitat delineation difficult. Upright inactive chimneys were colonized by stalked barnacles (*Vulcanolepas* cf. *parensis*; Figure 9E), shrimp (*Chorocaris vandoverae*), and galatheid squat lobster (*Munidopsis lauensis* and *M. starmer*). Numerous ophiuroid brittle stars were also observed in sediments at the base of some inactive sulfide mounds and rubble areas.

Nat Nat

Dimpled deep-sea sediment was observed among small (< 1 m) and large (>1 m) outcrops of inactive chimney rubble. Sediment-covered rubble was covered by hydroids (*Acryptolaria* sp., *Halecium* n. sp. 1, *Stegolaria geniculata*, *Sertularella* n. sp.), with branching bamboo coral (~ 2 per m^2; *Keratoisis* sp.) and sparse anemones (cf. *hadalanthus* sp.; Figure 9D). A few small outcrops were completely covered in carnivorous sponges (*Abyssocladia dominalba*; Figure 9A).

Fullagar Extended

Fullagar Extended is an area of closely spaced and intergrading active and inactive sulfide mounds and chimneys. Inactive sulfide mounds were covered by hydroids (*Acryptolaria* sp., *Halecium* n. sp. 1, *Stegolaria geniculata*, *Sertularella* n. sp.), and carnivorous sponges (*Abyssocladia dominalba).* Occasional galatheid squat lobsters (*Munidopsis lauensis* and *M. starmer*), shrimp (*Lebbeus* sp.), crabs (*Paralomis* cf. *spinosissima),* chimaeras, and zoarcid fish were also observed (Figure 9F).

Binns

Inactive sulfide areas are interspersed between large active forests and consist of fallen chimney rubble, as well as tall upright remnant chimneys <1 m to >10 m) with castle-like pinnacles. Inactive chimney rubble showed slight sediment coverage,

with high biomass of stalked barnacles, shrimp (*Chorocaris vandoverae*), and galatheid squat lobsters (*Munidopsis lauensis and M. starmer*).

Paine

The northwest portion of Paine is typical flat deep-sea seafloor with dimpled sediment tapering to a steep slope. Inactive chimney rubble was observed in fairly small clusters (< 1 m^2) in the central portion and southeast region of Paine. Biomass on the sulfide rubble was dominated by hydroids and galatheid squat lobsters. Inactive fallen chimneys (1 to 3 m height) were draped with sediment and were colonized by galatheid squat lobsters and hydroids. Many areas of inactive chimney rubble were almost completely covered with sediment (Figure 9B).

99

Site 99 is the sample site most peripheral to the active vents; no active venting was observed in 99. Sulfide rubble on ponded sediment at the southern end of 99 was dominated either by hydroids (*Acryptolaria* sp., *Halecium* n. sp. 1, *Stegolaria geniculata*, *Sertularella* n. sp.) or a mix of hydroids and and branching bamboo coral (*Keratoisis* sp.) colonized by numerous small, pink anemones (cf. H*adalanthus* sp.). High coral biomass was even observed in areas where sulfides were completely covered in sediment. Large anemones (*Actinosctyphia* cf. *saginata*; Figure 9C) were occasionally observed on the sulfides. Areas of large fallen chimneys were colonized by live bamboo corals (*Keratoisis* sp.), hydroids, as well as skeletonnes of corals

(*Keratoisis* sp.). Coral skeletonnes were colonized by hydroids (*Acryptolaria* sp., *Halecium* n. sp. 1, *Stegolaria geniculata*, *Sertularella* n. sp.) and small pink anemones (cf. *HManuensisadalanthus* sp.). Rarely, carnivorous sponges (*Abyssocladia dominalba*) and branching bamboo coral (*Keratoisis* sp.) were observed together.

Williamson

Bamboo corals (*Keratoisis* sp.) dominated inactive sulfide mounds at Williamson. Corals were observed on sulfide outcrops with low to medium sediment coverage. Hydroids were observed sharing the substratum with bamboo corals and occasionally growing on the corals themselves. Small pink anemones (cf. *hadalanthus* sp.) were also observed growing on branches of bamboo coral. Small inactive sulfide rubble areas with much less sediment coverage were not colonized by bamboo corals but were instead inhabited by dense populations of carnivorous sponges (*Abyssocladia dominalba*). Galatheid squat lobsters were observed in both habitats.

Active sample locations

There were six actively venting sample locations. Of the six active locations, the Binns and Kowalczyk fields were the most active and supported the highest biomass and abundance of vent-endemic taxa. At Fullagar Extended, there were a few localized areas of active venting and high biomass/abundance. Williamson, Paine,

and Nat Nat were the least active of the active sites, with the exception of the border between Nat Nat and Kowalczyk.

Binns

Binns was a very active area with many clear diffuse-flow chimneys (<3 m to >10 m) covered in provannid gastropods (*Alviniconcha* sp.1, *Ifremeria nautilei*), limpets (*Lepetodrilus schrolli, Olgasolaris tollmani*) and sessile barnacles (*Eochionelasmus ohtai cf. manuensis*), as well as black smokers (~296°C; Figure 8D, E). Active chimneys were tall, thin, and fragile, with castle-like peaks covered with white bacterial mats (Figure 8F). Areas of shimmering water and abundant shrimp (*Chorocaris vandoverae*) were observed, together with provannid gastropods (*Alviniconcha* sp.1, *Ifremeria nautilei*), bythograeid crabs (*Austinograea alayseae*), and galatheid squat lobsters (*Munidopsis lauensis* and *M. starmer*). Sessile barnacles (*Eochionelasmus ohtai* cf. *manuensis*) colonizing active chimneys and polynoid scale worms were observed crawling along the sides of active chimneys.

Kowalczyk

Abundant active black smokers indicated that Kowalczyk is an extremely active hydrothermal vent site. Black smoker chimneys were characterized by white bacterial mats covering the peaks (Figure 8A), with provannid gastropods (*Alviniconcha* sp.1, *Ifremeria nautilei*), limpets (*Lepetodrilus schrolli, Olgasolaris tollmani*), galatheid squat lobsters (*Munidopsis lauensis* and *M. starmer*), and

bythograeid crabs (*Austinograea alayseae*) occupied the lower portions of the chimneys. Many of the large active chimneys (greater than or equal to 8 m height) were completely encrusted with sessile barnacles (*Eochionelasmus ohtai* cf. *Manuensis*; Figure 10A,D). Barnacle-encrusted chimneys were also occupied by the biomass dominant provannid gastropods (*Alvinoconcha* sp.1 and *Ifremeria nautilei*), but the gastropods occurred in small patches rather than the large aggregations typical of non-barnacle-encrusted active chimneys in the area (Figure 10A,B). Individuals of *Eosipho desbruyeresi* crawled over barnacles very high up on the active chimneys at Kowalczyk.

Fullagar Extended

Active black smoker chimneys and clear-diffusing vents were colonized by yellow bacterial mats, galatheid squat lobsters (*Munidopsis lauensis* and *M. starmer*), provannid gastropods (*Alviniconcha* sp.1, *Ifremeria nautilei*), limpets (*Lepetodrilus schrolli, Olgasolaris tollmani*), bythograeid crabs (*Austinograea alayseae*), and anemones (*Tealidium* or *Bathydactylus*). Some chimneys no longer emitted high temperature fluids but were encrusted with live sessile barnacles (*Eochionelasmus ohtai* cf. *manuensis*) and harbored an occasional buccinid gastropod (*Eosipho desbruyeresi*). Active chimneys were found only meters away from tall (> 10 m) inactive chimneys.

Williamson

Active areas harbored many black smokers (224°C), white smokers, and clear diffuse flowing vents. These areas of activity were similar in species composition, abundance, and biomass to Fullagar Extended. No active venting was found in the western portion of Williamson.

Paine

Active chimneys throughout Paine were wide connected spires with an abundance of vent endemic fauna, including provannid gastropods (*Alvinoconcha* sp.1, *Ifremeria nautilei*), limpets (*Lepetodrilus schrolli, Olgasolaris tollmanni, Shinkailepas tufari*), shrimp (*Chorocaris vandoverae*), galatheid squat lobsters (*Munidopsis lauensis, M. starmer*), anemones (*Tealidium or Bathydactylus*), and bythograeid crabs (*Austinograea alayseae*). Active chimneys with lower biomass were colonized by sparse patches of sessile barnacles (*Eochionelasmus ohtai* cf. *Manuensis*), galatheid crabs (*A. alayseae*), and shrimp (*C. vandoverae*). Active zones were relatively close to inactive zones (~10 m). Unusual features of the Paine field were inactive chimneys (fallen or upright) with large numbers (> 100) of dead provannid snail shells (*Alviniconcha* sp.1 and *I. nautilei*) at or near (within 3 m) the base of the chimneys. Thread-like fissures on these chimneys appeared to be colonized by white bacteria. Scattered patches of live sessile barnacles (*E. ohtai cf. manuensis*), occasional shrimp (*C. vandoverae*), and/or scavenging galatheid squat lobsters (*M. lauensis, M. starmer*) were also observed on the chimneys (Figure 10C).

Dead and live provannid gastropods (*Alviniconcha* sp.1 and *I. nautilei*) on the chimneys appeared to be scavenged by bythograeid crabs (*A. alayseae*), galatheid squat lobsters (*M. lauensis, M. starmer*), and shrimp (*C. vandoverae*).

Nat Nat

Active hydrothermal chimneys were mainly observed along the border between Nat Nat and Kowalczyk. Active chimneys were short and stout, with unusually shaped, bulbous pinnacles (Figure 8B) or thin imbricated outflow layers (Figure 8C) at the summits. These chimneys were covered with white bacteria and dispensed a clear vent fluid. A few extremely thin, tall, finger-like chimneys (9-10 m height) were observed with patches of provannid gastropods in the shimmery water zone. Immense chimneys encrusted with sessile barnacles (*Eochionelasmus ohtai* cf. *Manuensis*) were found in Nat Nat, but in fewer numbers than at Kowalczyk. Only a few small clusters (<10 individuals) of provannid gastropods (*Alviniconcha* sp.1 and *Ifremeria nautilei*) were observed crawling on the immense barnacle-covered chimneys.

Stable isotope composition

A total of 104 tissue samples from 18 species from active and inactive sulfide mounds were analyzed for carbon, nitrogen, and sulfide composition (Table 3). The most ^{13}C-depleted isotopic compositions were observed in the vent endemic provannid gastropods, *Alviniconcha* sp.1 ($\delta^{13}C$ mean = -26 ‰ ± 2.2) and *Ifremeria nautilei*

($\delta^{13}C$ = -25 ‰ ±1.3) (Figure 4). The most ^{13}C-enriched isotopic compositions were observed in biomass dominant species from inactive sulfide mounds [bamboo coral (*Keratoisis* sp.; $\delta^{13}C$ = -20.5 ‰ ±1.1), cladorhizid carnivorous sponges (*Cladorhiza abyssocola*; $\delta^{13}C$ = -18 ‰), stalked barnacle (*Vulcanolepas* cf. *parensis*); $\delta^{13}C$ = -21.6 ‰ ±1.2), hydroids [*Acryptolaria/Halecium /Stegolaria geniculata/Sertularella*; -21.7 ‰ ±0.6; (Figure 5)]. The $\delta^{15}N$ isotopic compositions of organisms collected from active sites ranged from 1.4 ‰ to 12.0 ‰. The $\delta^{15}N$ isotopic compositions of organisms collected from inactive sites ranged from 1.4 to 16.9 ‰ (Figure 6). The ranges of sulfur isotopic values for active and inactive vent invertebrates were similar (active: -9.4 ‰ to 8.9 ‰; inactive: -9.9 ‰ to 6.3 ‰ (Figure 7).

Stable isotope composition of invertebrates from active sulfide mounds

The overwhelming biomass dominant organisms at active hydrothermal vents in the Suzette vent field were the endosymbiont-bearing provannid gastropods, which had the most depleted $\delta^{13}C$ values (*Alvinoconcha* sp.1, -29 ‰ to -23 ‰; *Ifremeria nautilei*, -27 ‰ to -22 ‰; Figure 4). The $\delta^{13}C$ values of scavengers (*Austinograea alayseae, Munidopsis* spp., *Chorocaris vandoverae*) ranged from -24 ‰ to -19 ‰. Grazing limpets (*Lepetodrilus schrolli, Olgasolaris tufari*) living on shells of provannid gastropods (*Alvinoconcha* sp.1, *Ifremeria nautilei*) also showed intermediate values of $\delta^{13}C$, ranging from -22 ‰ to -20 ‰. Two sessile barnacle (*Eochionelasmus ohtai*) specimens were isotopically heavy ($\delta^{13}C$ = -22 ‰ to -21 ‰), while the rest of the *E. ohtai* specimens were isotopically light ($\delta^{13}C$ = -27 ‰ and -25

‰). A hydroid sample and the stalked barnacle *Vulcanolepas* cf. *parensis* had $\delta^{13}C$ values almost identical to those of the same taxa collected from inactive sulfide mounds (-22 ‰ to -21 ‰). *Eosipho desbruyeresi*, a predatory gastropod had a $\delta^{13}C$ value of -28 ‰.

The $\delta^{15}N$ isotopic compositions of endosymbiotic-bearing provannid gastropods collected from active hydrothermal vents were depleted in ^{15}N (*Alviniconcha* sp.: $\delta^{15}N$ = 5.0 ‰ ±1.0; *Ifremeria nautilei*: $\delta^{15}N$ = 4.2‰ ±1.7; Figure 6). Grazing limpets (pooled samples of *Lepetodrilus* and *Olgasolaris*) had nitrogen isotopic values similar to those of the provannid gastropods ($\delta^{15}N$ = 4.8 ‰ ±1.3). Suspension feeders (*Eochionelasmus ohtai* cf. *manuensis*, *Vulcanolepas* cf. *parensis*, and a hydroid (likely *Acryptolaria, Halecium, Stegolaria geniculata, or Sertularella*) showed enriched ^{15}N values, ranging from 5 ‰ to 11 ‰ (8.5 ‰ +/- 2.0). Mobile scavengers (*Chorocaris vandoverae*, *Austinograea alayseae*, *Munidopsis spp.*) from active vent sites had only slightly enriched ^{15}N values (6 ‰ to 12 ‰), compared to suspension feeders (~1 ‰). The predatory gastropod *Eosipho desbruyeresi* had a $\delta^{15}N$ isotopic composition of 9.1 ‰.

Sulfur isotopic values for vent invertebrates from active sulfide mounds ranged from -9.4 ‰ to 8.9 ‰. Sulfur isotopic composition of inorganic material in active sulfide chimney substratum ranged from -2.6 ‰ to 1.1 ‰ (Figure 7).

Stable isotope composition of invertebrates from inactive sulfide mounds

The overwhelming biomass dominant organisms at inactive hydrothermal vents in the Suzette vent field were the suspension-feeding bamboo coral (*Keratoisis* sp.), stalked barnacle (*Vulcanolaepas* cf. *parensis*), hydroids, and a predatory carnivorous sponge (*Abyssocladia dominalba*; Figure 5). These dominant invertebrates had ^{13}C enriched $\delta^{13}C$ values that ranged from -23 ‰ to -18 ‰. Carbon isotopic compositions of suspension feeders (*Vulcanolepas* cf. *parensis*, hydroids, *Keratoisis* sp., cf. *hadalanthus* sp.) typically fell within that same range (-23 ‰ to -18 ‰), except for one hydroid outlier falling at -5 ‰ (not included in figure). Carbon isotopic compositions of mobile scavengers collected from inactive sulfide mounds (*Chorocaris vandoverae*, asellota isopod, *Munidopsis* spp, *Ventiella* cf. *sulfuris*) ranged from -23 ‰ to -21 ‰. For *C. vandoverae* and *Munidopsis* spp., these carbon isotopic compositions are similar to those measured in individuals collected from active mounds (-24 ‰ to -19 ‰). Predatory sponges (*Cladorhiza abyssicola, Abyssocladia dominalba*) were the most enriched in ^{13}C and ranged from -21 ‰ to -18 ‰. Carbon isotopic composition of tissues from deposit-feeding taxa, the brittlestar (*Ophiacantha* sp.) and the holothurian (*Chiridota hydrothermica*), ranged from -26 ‰ to -22 ‰.

Suspension feeders from inactive sulfide mounds (*Keratoisis* sp., cf. *hadalanthus* sp., *Vulcanoleapas* cf. *parensis*, and a hydroid) were enriched in ^{15}N, ranging from 7 ‰ to 17 ‰. Mobile scavengers (*Chorocaris vandoverae*, *Munidopsis spp.*, *Ventiella* cf. *sulfuris*, asellota isopod) from inactive sulfide mounds had $\delta^{15}N$

values that ranged from 1.4 ‰ to 12.5 ‰. Two predatory carnivorous sponges were collected from inactive sulfide mounds (*Cladorhiza abyssocola, Abyssocladia* dominalba) and were enriched in ^{15}N, (9.9 ‰ to 13.9 ‰). The deposit feeder *Chiridota hydrothermica* was depleted in ^{15}N (3.1 ‰ to 5.4 ‰; Figure 6), but *Ophiacantha* sp. was enriched in ^{15}N (11.1 ‰). The $\delta^{34}S$ for inactive vent invertebrates ranged from -9.93 to 6.28 ‰, with inorganic sulfides associated with sulfide substrate samples from inactive chimneys ranging from -3.3 ‰ to 3.8 ‰ (Figure 7).

DISCUSSION

Dominant taxa of Manus Basin and their biogeographic relationships with taxa of other western Pacific back-arc basin vents

Dominant invertebrates at active vent chimneys

Biogeographic analyses through comparisons of species lists help to identify species that might be endemic to a particular locale and thus might be especially susceptible to extinction. Two key factors, broad distributions and large population densities, are necessary for a species to have low risk of extinction. These factors ensure a species is likely to survive in the face of local degradation of habitat as hydrothermal activity wanes. Genus or family level comparisons provide insight into evolutionary links and potential corridors for species dispersion. Biogeographic

analyses need to be considered in estimates of population densities as well as critical biological and environmental interactions that influence survival of species.

At the species level, invertebrates from active chimneys of the Manus Basin, are most closely related to that of North Fiji and Lau Basin vents (Desbruyeres et al. 2006). The biomass dominant invertebrates typical of active hydrothermal chimneys in the Suzette vent field are the vent endemic provannid gastropods (*Alviniconcha* sp.1, *Ifremeria nautilei*). The genus *Alviniconcha* is widespread throughout vents in the western Pacific, and a single, undescribed species (referred to in the literature as *Alviniconcha* sp. 1) is known from both Manus Basin and North Fiji Basin (Kojima et al. 2001a). Our molecular sequences confirm that specimens collected from the Suzette vent field in Manus Basin belong to *Alviniconcha* sp. 1, but we did not analyze sufficient number of individuals to evaluate the degree of genetic exchange between Manus and North Fiji Basins.

Ifremeria nautilei is the other dominant gastropod of the Suzette vent field, Manus Basin and is widespread throughout the western Pacific (i.e., North Fiji and Lau Basins; Borowski et al. 2002). Mitochondrial DNA sequences of *I. nautilei* from Manus and North Fiji Basins, reported by Kojima et al. (2000), showed they shared no common haplotypes, indicating that the populations in the two basins are genetically isolated, although this isolation is believed to be relatively recent (Kojima et al. 2000).

Other biomass dominant invertebrates known from the Manus Basin are the vesicomyid clams and bathymodiolid mussels, but these bivalves were not observed

in the Suzette vent field. Vesicomyid clams are often found at hydrothermal vent sites in the eastern and northeastern Pacific (Hashimoto et al. 1999, Kojima et al. 2004) but they have currently only been found in two sites in the southwestern Pacific: DESMOS, Manus Basin and the nearby Edison Seamount vent site (located on the east side of the New Ireland Island from Manus Basin; Hashimoto et al. 1999). There are also two mussel species (*Bathymodiolus brevior, Bathymodiolus* sp.) that have been described from Manus Basin (*Bathymodiolus brevior, Bathymodiolus* sp.) but neither group of invertebrates was observed at active hydrothermal vents within Suzette vent field.

The charismatic tubeworms, which tend to garner a lot of attention, are known from the Manus Basin; however, they were not observed in the Suzette vent field. Manus Basin is not known for an abundance of tubeworms (Galkin 1997), but it is an area that hosts high tubeworm diversity, with four of the seven known clades reported within Manus Basin (lamellibrachiids, escarpiids, arcovestiids, and *Alaysia*-like tubeworms) and up to five species [*Escarpia* sp. E2, *Lamellibrachia* sp. L4, *Ridgeia* sp., *Alaysia* sp. A4 (Hashimoto et al. 1999), *Arcovestia ivanovi* (Southward & Galkin 1997)]. The lack of biomass dominant bivalves and tubeworms in the Suzette vent field is not believed to be sampling artifact, but rather represents a lower diversity site.

Dominant invertebrates of inactive sulfide mounds

Biomass dominant invertebrates typical of inactive sulfide mounds within the Suzette vent field were characterized by branching bamboo coral (*Keratoisis* sp.). This genus belongs to a diverse subfamily (Keratoisidinae), best known from deep-water trawling of seamounts in the southwestern Pacific (Smith et al. 2004). Concerns about loss of biodiversity in this group is already heightened due to poorly known systematics, limited collections (Smith et al. 2004) and few genetic data (especially on the family Isididae, subfamily Keratoisidinae; France & Hoover 2002). Bamboo corals were previously assumed to be endemic to seamounts; however, recent collections suggest otherwise [i.e., occurrences from Mid-Atlantic, off the Eastern Scotian Shelf (Grass & Willison 2005), areas in the northeast and northwest Pacific (Richer de Forges et al. 2000, Smith et al. 2004), the present study in the Suzette Vent Field, as well as recent collections from flat topographies distributed around New Zealand (Smith et al. 2004)].

In general, deep-sea corals are long lived, hundreds or even thousands of years (Andrews & Cordes 2002), and provide habitat for a large number of invertebrate and fish species. The slow growth patterns make them especially susceptible to human activities that damage the seafloor. A recent age study by Andrews and Calliet (2005) of bamboo coral from the Davidson Seamount, suggests that from a cross section 8 to 11 mm in radius, an estimate of approximately 220 years in age would be likely.

Threats to deep-sea corals such as bottom trawling for commercially valuable fish, oil and gas exploration and extraction, cable laying, mineral extraction, and bioprospecting do terrible damage to these communities that need decades to millennia to recover (Rogers 1999, Freiwald & Fossa 2004). Similar to old-growth forests on land, coral communities are easily disrupted and once lost, so are the diverse, complex habitats that they sustained.

Numerically dominant invertebrates found at inactive sulfide mounds within the Suzette vent field include the stalked barnacle (*Vulcanolepas* cf. *parensis; Neolepas* cf. *zevinae*), hydroids (*Acryptolaria* sp., *Halecium* n. sp. 1, *Stegolaria geniculata*, *Sertularella* n. sp.), and a carnivorous sponge (*Abyssocladia dominalba*). Interestingly, *Vulcanolepas parensis* from the volcanically active areas on the Pacific-Antarctic Ridge is believed to be vent endemic (Buckeridge 2000, Southward & Jones 2003). *Neolepas zevinae* has been observed at the east Pacific Rise and *Neolapas sp.* has been noted from the Indian ocean (Buckeridge 2000, Southward & Jones 2003). *Abyssocladia dominalba* has only recently been reported from north Fiji (White Lady site) and was also observed on inactive sulfide mounds (Auzende et al. 1989, Desbruyeres et al. 1994).

Inactive sulfide mounds also serve as habitat for active vent-associated fauna: sessile barnacle (*Eochionelasmus ohtai* cf. *manuensis*), bythograeid crab (*Austinograea alayseae*), alvinocarid shrimp (*Chorocaris vandoverae*), and galatheid squat lobsters (*Munidopsis starmer, M. lauensis*). With the exception of the barnacles (*E. ohtai* cf. *manuensis*), these invertebrates are all decapods and mobile scavengers

or omnivores. They can move between active and inactive habitats, especially in locations where active and inactive habitats are within close proximity (i.e., meters) within the vent fields. The vent adapted *Austinograea alayseae* has been noted by Galkin (1997) to crawl among active vent openings but also to scavenge at inactive sulfide mounds. The shrimp, *Chorocaris vandoverae*, another vent-adapted invertebrate, is associated with vent opening and believed to feed on encrusting bacteria growing on substrate as well as the vent invertebrates themselves (Van Dover et al. 1988, Galkin 1997). This shrimp may also be found scavenging at inactive sulfide chimneys. Although galatheid squat lobsters are not present at vent openings, they are associated with the peripheral vent areas and have been known to venture into inactive chimneys sites.

Nutritional resources at inactive vents

Three non-exclusive conditions were considered during this research (1) low-level venting of hydrothermal fluids could actually be continued at these "inactive" sites, supporting chemoautotrophic production within the overlying water column; 2) *in situ* production of organic carbon from acid-labile sulfides mobilized by microbial activity to support primary production (chemoautotrophic); 3) the topographic relief may change the local flow regime of the mounds, concentrating suspended particulates for the biota to feed upon (either chemosynthetic from near by active sites, or photosynthetic, from sinking particles.

While it is routine to observe megafauna and macrofauna associated with inactive sulfide mounds, it is not understood what accounts for such high biomass in these areas compared to the rest of the deep sea. The role of microbial primary production (based on oxidation of mineral sulfides) in the nutrition of these animals, opens up the possibility that these communities have a unique chemosynthetic primary production. Assuming true "inactivity", we will disregard condition number one (which will be discussed in detail later), leaving conditions 2) *in situ* production of organic carbon from acid-labile sulfides mobilized by microbial activity and 3) topographic relief concentrating suspended particulates (photosynthetic or chemosynthetic).

When deep-sea hydrothermal activity stops, chimney structures that are enriched with particulate metal sulfides continue to provide microbes access to necessary inorganic chemicals and continue to interact with the seawater (Edwards et al. 2000, Suzuki et al. 2004). Metal sulfide oxidation can provide enough energy for microbial chemoautotrophic production on the surface and subsurface layers of inactive sulfide mounds (Edwards et al. 2000, Suzuki et al. 2004).

In regard to topographic relief, it has been hypothesized that upwelling due to abrupt topography enhances primary production and consumer biomass (Uda & Ishino 1958). Physical models, observations, and direct measurements suggest that the topography of seamounts affects current regimes (Uda & Ishino 1958, Genin et al. 1986, Dower & Perry 2001). Vortex lines are compressed and there is a change in potential vorticity inducing anticyclonic (counterclockwise in southern hemisphere

and clockwise rotation in northern hemisphere) motion. This quasi-stationary eddy is known as the Taylor column and is thought to be able to remain trapped above the seamount indefinitely (Taylor 1923, Genin 2004).

This type of velocity pattern has been observed at the Jasper Seamount and is hypothesized to explain coral distributions (Genin et al. 1986). Patterns of abundance of the black coral, *Stichopathes* sp. are associated with local topography on three different levels:

1) densities are higher near the peaks relative to the entire seamount.

2) densities among peaks have two distribution patterns: narrow peaks show higher densities at the crest while wider peaks show higher densities along the crest edge.

3) densities are higher on the pinnacles and knobs of the individual peaks

The high abundance of black coral observed is believed to be due to current patterns (1400 m to 3900 m; Genin et al. 1986). The intensified water flow around peaks can be explained by the process of upwelling i.e., when currents encounter wide topographic mounds, water moves up and over the summit. Speeds of water flow at the peak are typically double that of the slope because the upwelling requires acceleration over the top of the seamount (Genin et al. 1986). Food concentration and larvae could vary at different inactive sites due to topographic effects on water flow and to added local current regimes from active venting within close proximity (Genin et al. 1986).

Free-living bacteria suspended in vent effluents and encrusting mats that may break loose from the substratum provide food particles for suspension feeders at vents. Centripetal flow of thermal convection cells may also enhance the delivery of photosynthetically derived detritus and therefore may also contribute to the nutrition of suspension feeders at and near vents (Enright et al. 1981, Galkin 1997). Concentrations of non-vent-endemic anemones, hydroids, brisingid seastars, and gorgonians have been observed to prefer high exposed areas such as inactive sulfide mounds, and have been used as a resource for finding active vent areas (Galkin 1997).

Our stable isotope results suggest there is a contribution of a chemosynthetic food source for invertebrates colonizing inactive sulfide mounds in Manus Basin. Chemoautotrophic bacteria are generally isotopically distinct from phytoplankton. The accepted photosynthetic range for $\delta^{13}C$ is typically -22 ‰ to -15 ‰ (Gearing et al. 1984, Van Dover & Fry 1989, Conway et al. 1994, Fisher et al. 1994, Colaco et al. 2002). The chemosynthetic range is slightly more complex as there is large dichotomy in composition observed between ^{13}C-enriched tissues of the vestimentiferan (-9 ‰ to -16 ‰) and the extremely ^{13}C-depleted value of the bivalves which fall around -33 ‰ (Rau & Hedges 1979, Rau 1981a, Market et al. 2007). This is believed to be explained by 1) which enzyme form is used during carbon fixation via the Calvin cycle 2) use of two different carbon fixation pathways (i.e., Calvin cycle and reverse tricarboxylic acid cycle).

During carbon fixation via the Calvin cycle expression of form I Rubisco enzyme results in much more depleted $\delta^{13}C$ (bivalves) and expression of Rubisco

form II results in much more enriched $\delta^{13}C$ values (vestimentiferans; Robinson & Cavanaugh 1995). The reverse tricarboxylic acid cycle (rTCA) is, at least partly, thought to be used in symbiont carbon fixation and represents an alternative carbon fixation mechanism that requires less energy than the Calvin cycle (i.e., acetyl CoA is synthesized by the incorporation of 2 carbon dioxides, not breaking down acetyl CoA with the release of 2 carbon dioxides, resulting in more ATP; Market et al. 2007).

A recent study involving the tubeworm *Riftia pachyptila*, suggest that this species may be able to adjust the production of enzymes (needed for energy metabolism) to their environmental conditions (Market et al. 2007). This advocates that the *Riftia pachyptila* symbiont might be switching between the rTCA cycle and the Calvin cycle depending on the high or low energy situation in the environment (i.e., Calvin cycle might be reduced in favor of the energetically favorable rTCA cycle; Market et al. 2007).

If the use of two carbon fixation pathways (rTCA and calvin cycle) explain the long-standing dilemma of two isotopically distinct ranges of $\delta^{13}C$ between vestimentiferans and bivalves, it is possible that other deep-sea organism may be utilizing the same or other carbon fixing pathways.

Stable isotopes

Carbon

Given the close proximity of the inactive sites to active sites in the Suzette vent field it is likely that the invertebrates (inactive as well as active) are exposed to a

complex mixture of autotrophic (chemosynthetic) and heterotrophic (photosynthetic) cells/debris. From this we can draw some inferences about the resulting intermediate values of the invertebrates and the composition of their food source. Active and inactive vent invertebrates had $\delta^{13}C$ values that overlapped (Figure 4, 5), resulting in ambiguous intermediate values. Multiple sources of detritus entering a system are believed to produce intermediate $\delta^{13}C$ values (Van Dover & Fry 1994, Van Dover 2002); mostly those from a mixed diet of two isotopically extreme sources such as chemosynthetic and photosynthetic detritus (Fry & Sherr 1984, Van Dover & Fry 1994, Van Dover et al. 2002).

Species at vents are capable of selectively feeding (e.g., vent endemic primary consumers *Alviniconcha* sp. 1 and *Ifremeria nautilei*) but it is highly unlikely that most species of scavengers or suspension feeders can achieve such a high degree of selectivity. Even if inactive sulfide mounds were not exposed to large plume dispersals, scavengers such as *Chorocaris vandoverae*, *Austinograea alayseae*, *Munidopsis starmer and M. lauensis* (typically showing intermediate values) are mobile and move easily in and out of active and inactive sites, allowing easy access and consumption of multiple sources of detritus.

Nitrogen

Available sources of nitrogen at hydrothermal vents consist of seawater nitrogen, atmospheric nitrogen, seawater nitrate (NO_3^-), reduced ammonia (NH_3), and molecular nitrogen. Seawater nitrogen has a $\delta^{15}N$ of 0‰, as does atmospheric

nitrogen (Table 3; Peterson & Fry 1987, Conway et al. 1994). Readily available seawater nitrate (NO_3^-) has an $\delta^{15}N$ of +3 ‰ to +6% (Peterson & Fry 1987), whereas highly reduced ammonia (NH_3) has an $\delta^{15}N$ of > +6 ‰ (Saino & Hattori 1987). Essentially, if vent organism were using vent nitrogen sources their $\delta^{15}N$ values would range from -12 ‰ to +4 ‰ (Brooks et al. 1987, Van Dover & Fry 1989), lighter than ambient deep-sea invertebrates using deep-sea nitrogen sources (+3 ‰ to +6‰). However, secondary consumers such as crabs at hydrothermal vents have had $\delta^{15}N$ values as isotopically enriched as +10 ‰ (Rau 1981a) or just below +10 ‰ (Conway et al. 1994, Van Dover & Fry 1994). Compared to the results of these past studies, our $\delta^{15}N$ results appear to fit into expected values of active vent $\delta^{15}N$.

It is important to keep in mind that deep-sea sediment has a high variability in nitrogen concentration and nitrogen composition mainly due to diagenesis, remineralization/degradation and even size class of particulate organic matter. These detrital components need to be considered in trophic ecology for organisms at active and inactive vent areas and food web isotope analysis, but it is very difficult to account for these processes.

Sulfur

Sulfate reduction in the relatively oxic deep-sea sediments and pelagic waters is not prevalent (Berner 1972, Ruby et al. 1981), leaving much of the open-ocean low in reduced inorganic sulfur (Jannasch et al. 1974, Ruby et al. 1981). Hydrothermal spreading centers, however, produce high concentrations of geothermal H_2S (Corliss

et al. 1979, Ruby et al. 1981) providing a likely energy source for such densely populated ecosystems (Ruby et al. 1981). $\delta^{34}S$ values of -40 ‰ for sulfide minerals at vents is much more depleted (Conway et al. 1994), while sulfur from seawater sulfate has values around +20 ‰ (Conway et al. 1994). The average sulfur isotopic composition for tissues from invertebrates at inactive sulfide mounds, matches that of the inorganic sulfide in the inactive sulfide minerals. This suggests that invertebrates found at active and inactive sulfide mounds do not obtain their sulfide from marine algae but rather dissolved sulfides or sulfide minerals. This is based on observations that isotopic effects during oxidation of sulfide and elemental sulfur are approximately 1 ‰ (Fry et al. 1983, Vetter & Fry 1998).

Mining implications

Deep-sea corals, such as the branching bamboo coral (*Keratoisis* sp.) found at inactive sulfide mounds need a hard, rocky substrate on which to attach as larvae (Freiwald & Fossa 2004). Several factors limit where deep-sea corals will thrive: substrate type, current speed, seafloor relief (ruggedness of the seafloor), nutrient availability, and temperature (Rogers 1999, Freiwald & Fossa 2004, Kahng & Grigg 2005).

Mining of inactive sulfide mounds will greatly affect three of the above factors (substrate, seafloor relief, nutrient availability), resulting in at least habitat loss and local extinction of inactive sulfide mounds and the fauna that inhabits them. Resuspension of surface and subsurface sediments could also be an issue if allowed to

rain out onto the surrounding seafloor (Jumars 1981, Glover & Smith 2003) by burying hard substrate, surface and subsurface benthos, as well as covering the sediment-water interface with nutrient-poor sediments (Jumars 1981, Smith & Kauffman 1999, Glover & Smith 2003). If a vacuum device is used to minimize fallout, impact will be unknown until assessed. Even short-term resuspension of sediment, causing turbid waters, is believed to be detrimental to deep-sea corals (Freiwald & Fossa 2004). Nutrient-poor subsurface sediment that has been stirred up becomes the main food source and will yield stress to surface deposit feeders and hard substrate suspension feeders, known to populate much of the deep sea and inactive sulfide mounds (Glover & Smith 2003).

If mining continues for extended periods these nutrition stressors will be chronic and enhanced for these fauna. It must also be taken into consideration that mining of inactive sulfide mounds will also greatly impact active chimneys and vent communities, due to the close proximity of inactive sulfide mounds to active vent chimneys throughout the Suzette vent field.

Inactive versus active vents

Geologically, active deep-sea hydrothermal vents are defined as fractures or fissure in the sea-floor typically near a mid-ocean ridge or back-arc basin from which mineral-rich superheated water is emanating. But to fully define an active hydrothermal vent habitat, many parameters from different disciplines must be considered (i.e., biological, geological, chemical). High productivity and biomass of

vent endemic organisms, which are fueled by the inorganic chemicals dissolved in vent fluids, provide the extra detail necessary for a more accurate description. All of these parameters, however, are not always obtainable in extreme environments and while some observations seem rather straight forward (i.e., vent endemic taxa infers some hydrothermal venting even if it is not visible to the naked eye), others are subjective.

In reality, delineation between active hydrothermal vents and inactive sulfide mounds (such as Binns, Kowalczyk, Nat Nat, and Fullagar Extended in the Suzette vent field) is not clear cut. Black smokers, grey smokers, and clear diffusing vents are typically easily identified; however, there is an untidy distribution that lies between obvious active and inactive zones. Intermediate stages of activity are depicted by hydrothermal sediment, weak hydrothermal flow through cracks in chimneys, lava flows and pillows, and places where plumes reach waning chimneys and inactive sulfide mounds (Galkin 1997). Transition stages arise due to the waning of active hydrothermal chimneys and the successive stages make it impossible to provide a clear cut definition of inactive and active hydrothermal vents.

For organisms living in a deep-sea chemosynthetic environment the most important resources are the inorganic chemicals (e.g., H_2S, CH_4) provided by the environment and the microbes that fix inorganic carbon in order to provided them with organic carbon. Inactive sulfide mounds barely seeping vent fluid or completely inactive, possess both the microbes and inorganic chemicals, albeit in a slightly different form (particulate rather than dissolved sulfides). Our results indicate that

the invertebrate species colonizing inactive sulfide mounds are relying on chemoautotrphic microbes for at least some part of their nutrition. If other deep-sea habitats are also incorporating hydrothermal vent produced nutrients into their food chain, we may risk destroying vital microbial communities that may be relevant to the energetics of the deep-sea floor in ways that we have not yet come to appreciate.

FIGURE LEGENDS

Figure 1. Manus Basin, Papua New Guinea, showing Suzette, PACMANUS and SuSu Knolls (Adapted from Binns 2004).

Figure 2. Geology and location of Suzette vent field within SuSu knolls (Taken from Binns 2004).

Figure 3. Suzette vent field sample locations and site locactions.

Figure 4. Carbon stable isotopic composition of invertebrates from active vents. Symbols differentiate feeding type.

Figure 5. Carbon stable isotopic composition of invertebrates from inactive sulfide mounds. Symbols differentiate feeding type.

Figure 6. Nitrogen stable isotopic composition of organisms from active and inactive sites categorized by feeding type.

Figure 7. Sulfur stable isotopic composition of organisms from active and inactive sites and the substrate material collected from the active and inactive sulfide chimneys.

Figure 8. *In situ* photographs at active chimney sites; (A) active black smoker chimneys and clear diffusing vents were colonized by yellow bacterial mats. Representative image used from Kowalczyk; (B) chimney peaks characterized by white bacterial mats. Representative image used from Nat Nat; (C) a diffuse flowing vent with thin imbricated outflow layers. Representative image used from Nat Nat; D-E. typical active vent habitats dominated by *Alviniconcha hessleri* (D) and *Ifremeria* (E) representative image used from Binns); (F) castle-like peaks covered with white bacterial mats. Representative image used from Kowalczyk.

Figure 9. *In situ* photographs at inactive chimney sites; (A) Carnivorous sponges (*Abyssocladia dominalba*) covering a sulfide outcrop. Representative image used from Williamson; (B) Sulfide outcrops draped with sediment and colonized by branching bamboo coral (*Keratoisis* sp.). Representative image used from Paine; (C) sulfide mounds were covered by hydroids (*Acryptolaria* sp., *Halecium* n. sp. 1, *Stegolaria geniculata*, *Sertularella* n. sp.), and the occasional large anemone (*Actinosctyphia* cf. *saginata*). Representative image used from Nat Nat; (D) sulfide rubble dusted with sediment dominated by hydroids (*Acryptolaria* sp., *Halecium* n. sp. 1, *Stegolaria geniculata*, *Sertularella* n. sp.) and branching bamboo coral (*Keratoisis* sp.) Representative image used from 99; (E) Chimneys colonized by stalked barnacles (*Vulcanolepas* cf. *parensis*). Representative image used from Binns; (F) Inactive chimney outcrop inhabited by hydroids (*Acryptolaria* sp.,

Halecium n. sp. 1, *Stegolaria geniculata*, *Sertularella* n. sp.), branching bamboo coral (*Keratoisis* sp.) and small pink anemones (cf. *hadalanthus* sp), along with the sightings of shrimp (*Lebbeus* sp.), crabs (*Paralomis* cf. *spinosissima*) Representative image used from 99.

Figure 10. Intermediate stage; (A). large active chimneys completely encrusted with sessile barnacles (*Eochionelasmus ohtai* cf. *Manuensis*). Representative image used from Kowalczyk; (B) Barnacle encrusted chimney with individual provannid gastropods (*Ifremeria nautilei*) crawling on barnacles. Representative image used from Kowalczyk; (C) Representative image used from Williamson; (D) Active chimneys colonized by sparse patches of sessile barnacles (*Eochionelasmus ohtai* cf. *Manuensis*), provannid gastropods (*Alviniconcha* sp.1 and *I. nautilei*), galatheid crabs (*A. alayseae*), and shrimp (*C. vandoverae*). Representative image used from Paine.

Figure 1

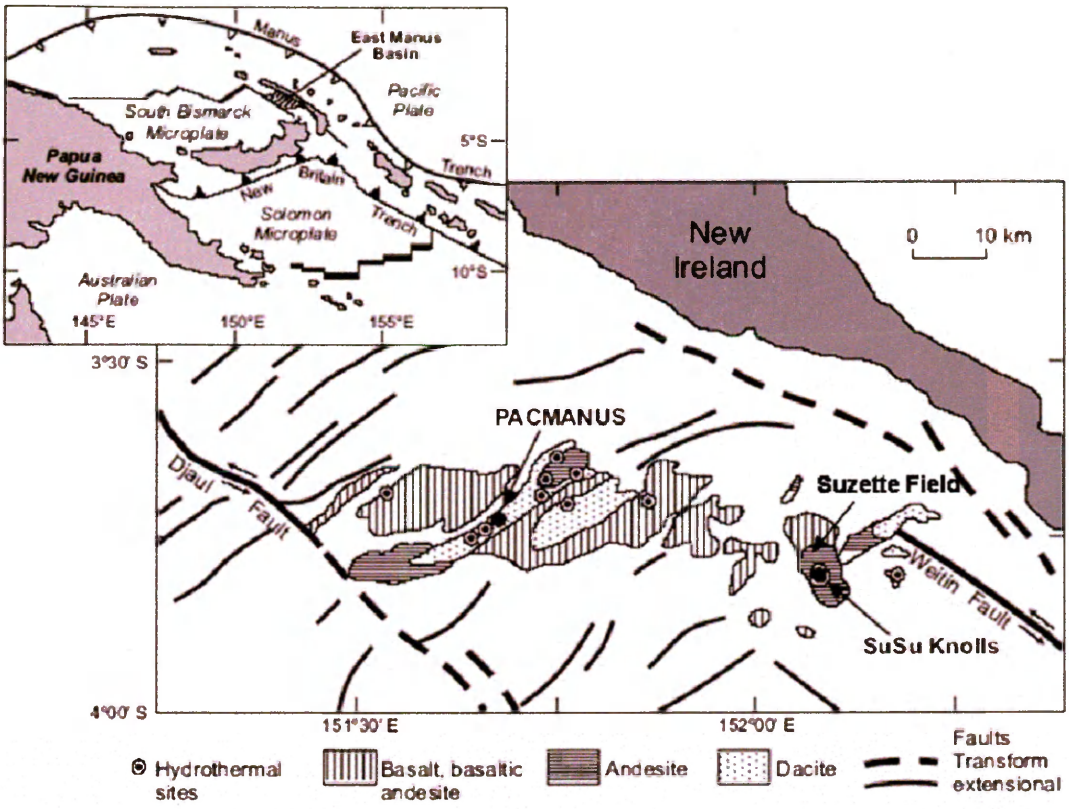

Manus
East Manus Basin
Pacific Plate
South Bismarck Microplate
Papua New Guinea
New Britain Trench
Solomon Microplate
Australian Plate
5°S
10°S
145°E
150°E
155°E
New Ireland
0 10 km
3°30' S
4°00' S
PACMANUS
Djaul Fault
Suzette Field
Weitin Fault
SuSu Knolls
151°30' E
152°00' E
Hydrothermal sites
Basalt, basaltic andesite
Andesite
Dacite
Faults
Transform
extensional

Figure 2

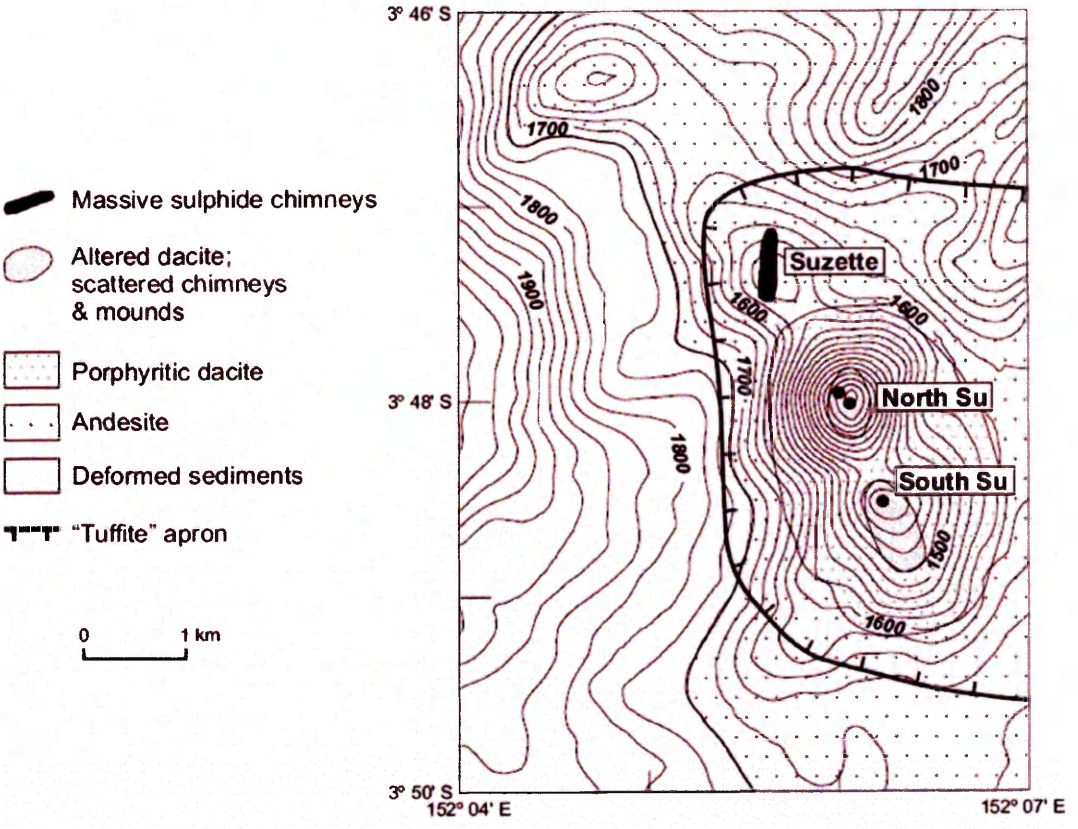

Massive sulphide chimneys
Altered dacite; scattered chimneys & mounds
Porphyritic dacite
Andesite
Deformed sediments
"Tuffite" apron
0
1 km
3° 46' S
3° 48' S
3° 50' S
152° 04' E
152° 07' E
Suzette
North Su
South Su
1700
1800
1900
1600
1500

Figure 3

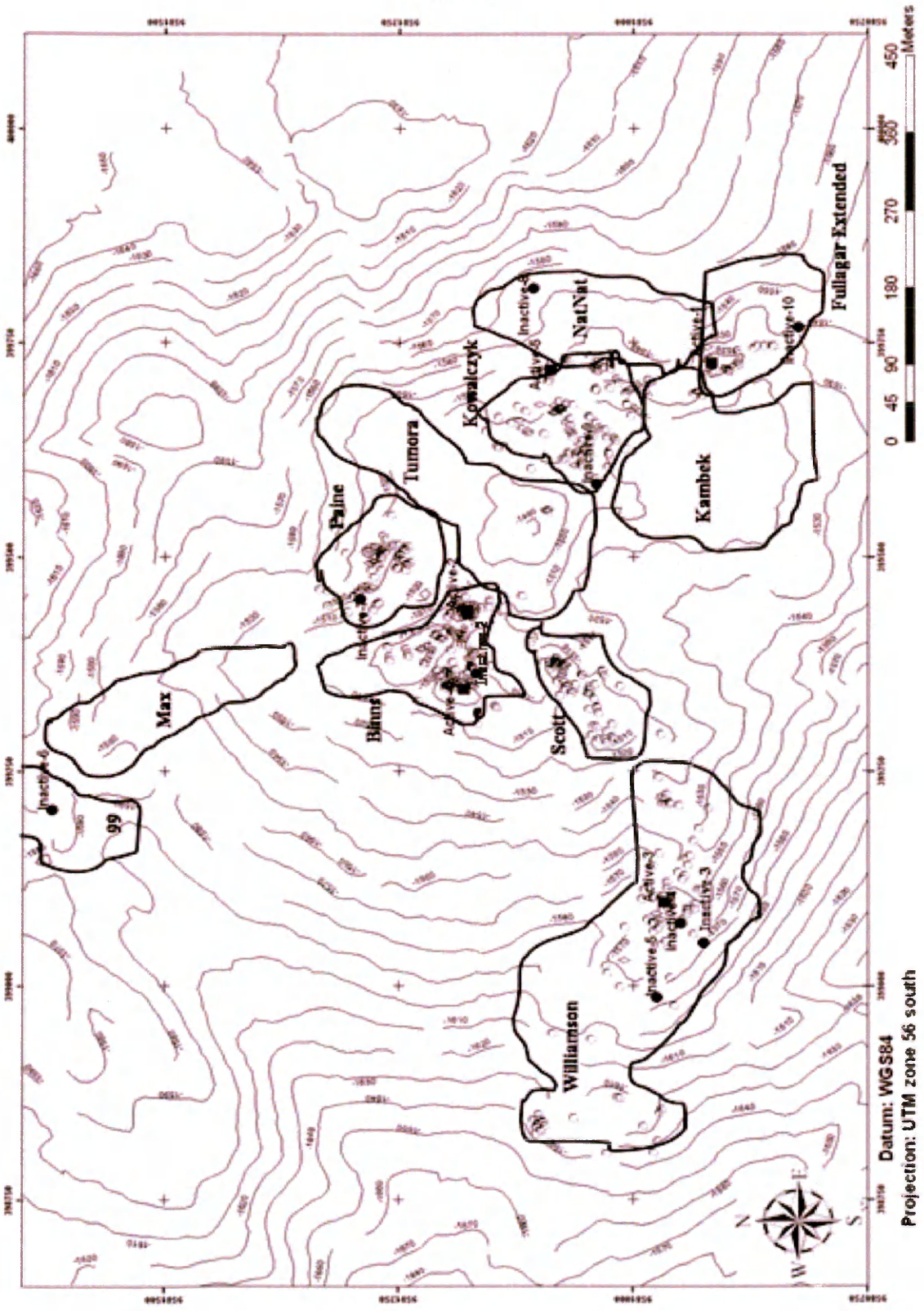

Pulliagar Extended
NatNat
Kowalczyk
Tumora
Paine
Kambek
Max
Blunt
Scott
Williamson
99
Inactive-6
Inactive-10
Inactive-3
Meters
450
360
270
180
90
45
0
Datum: WGS84
Projection: UTM zone 56 south

Figure 4

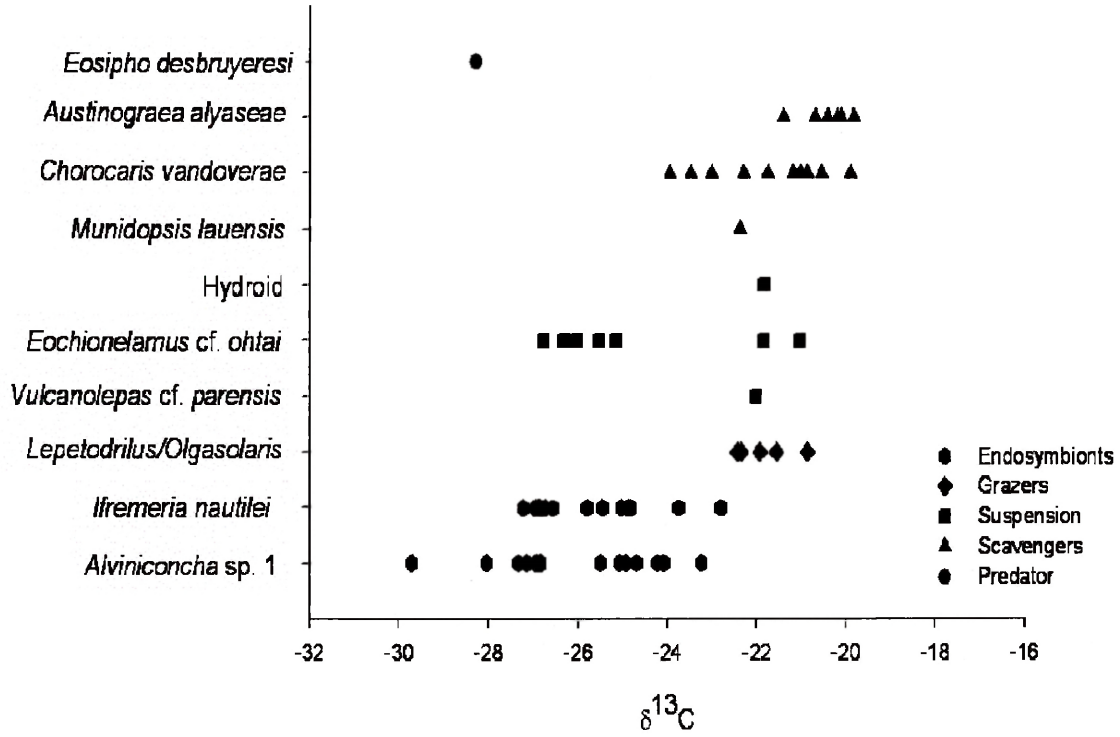

Eosipho desbruyeresi
Austinograea alyaseae
Chorocaris vandoverae
Munidopsis lauensis
Hydroid
Eochionelamus cf. ohtai
Vulcanolepas cf. parensis
Lepetodrilus/Olgasolaris
Ifremeria nautilei
Alviniconcha sp. 1
-32
-30
-28
-26
-24
-22
-20
-18
-16
δ13C
Endosymbionts
Grazers
Suspension
Scavengers
Predator

Figure 5

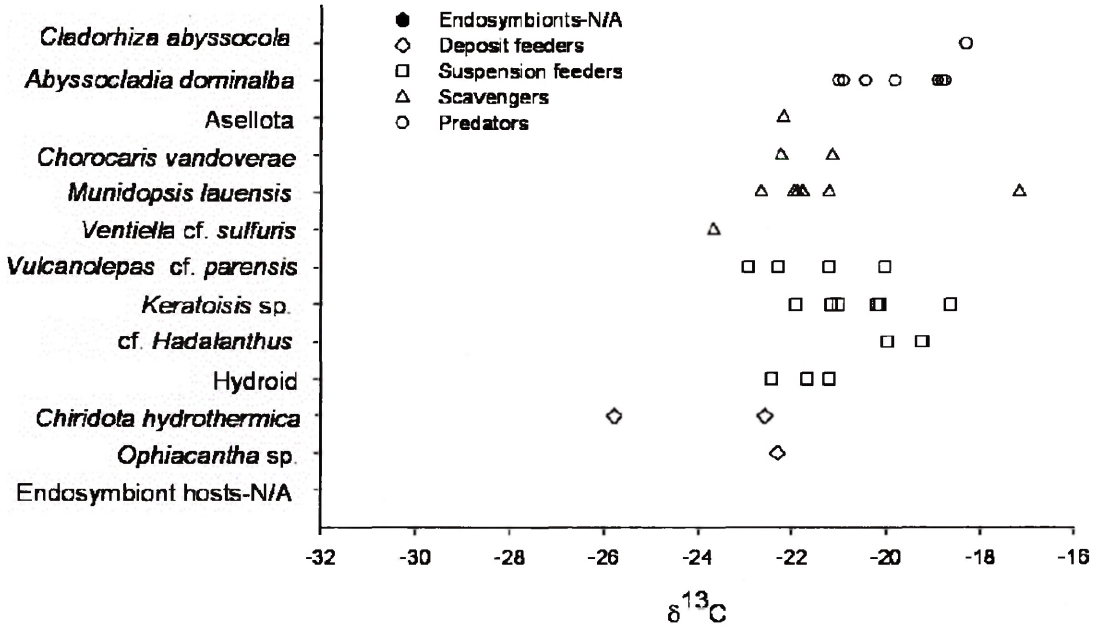

Endosymbionts-N/A
Deposit feeders
Suspension feeders
Scavengers
Predators
Cladorhiza abyssocola
Abyssocladia dominalba
Asellota
Chorocaris vandoverae
Munidopsis lauensis
Ventiella cf. sulfuris
Vulcanolepas cf. parensis
Keratoisis sp.
cf. Hadalanthus
Hydroid
Chiridota hydrothermica
Ophiacantha sp.
Endosymbiont hosts-N/A
-32
-30
-28
-26
-24
-22
-20
-18
-16
δ13C

Figure 6

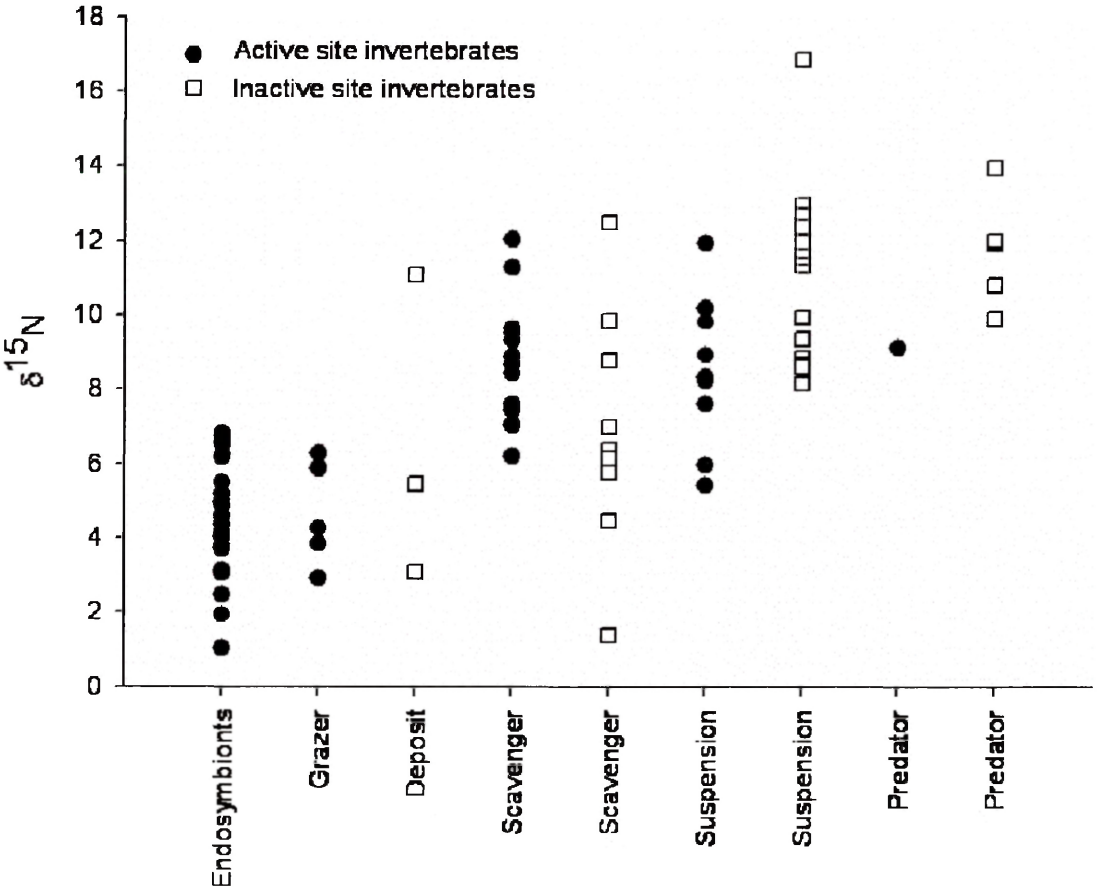

Active site invertebrates
Inactive site invertebrates
δ15N
18
16
14
12
10
8
6
4
2
0
Endosymbionts
Grazer
Deposit
Scavenger
Scavenger
Suspension
Suspension
Predator
Predator

Figure 7

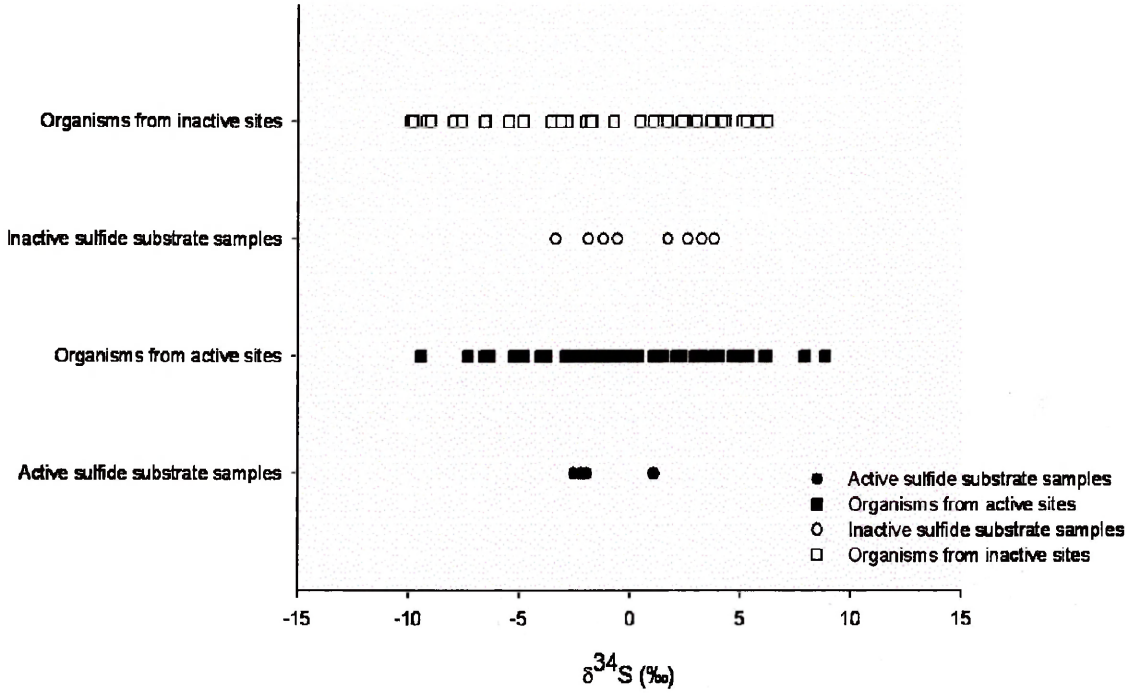

Organisms from inactive sites
Inactive sulfide substrate samples
Organisms from active sites
Active sulfide substrate samples
-15
-10
-5
0
5
10
15
δ34S (‰)
Active sulfide substrate samples
Organisms from active sites
Inactive sulfide substrate samples
Organisms from inactive sites

Figure 8

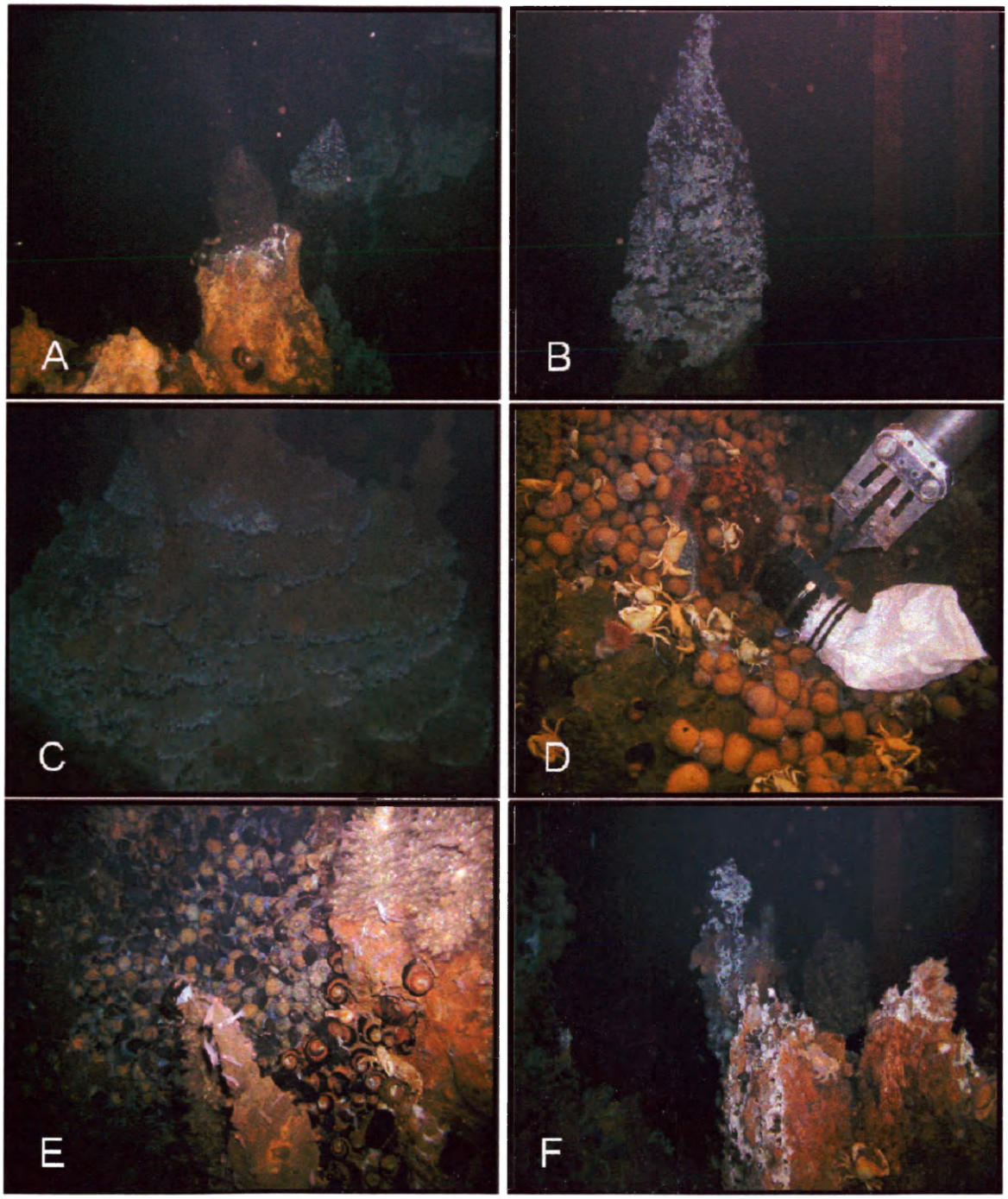


Figure 9

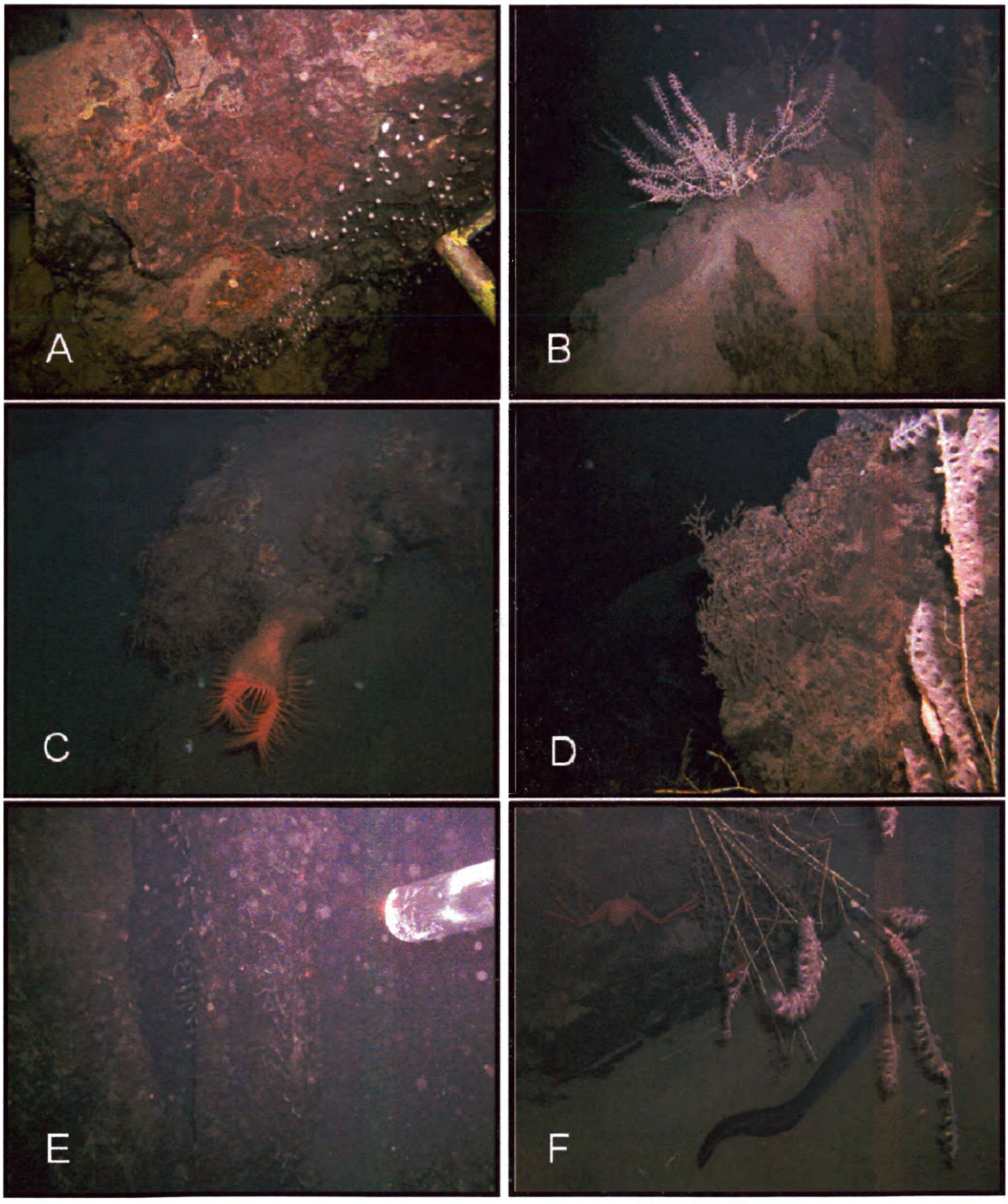


Figure 10

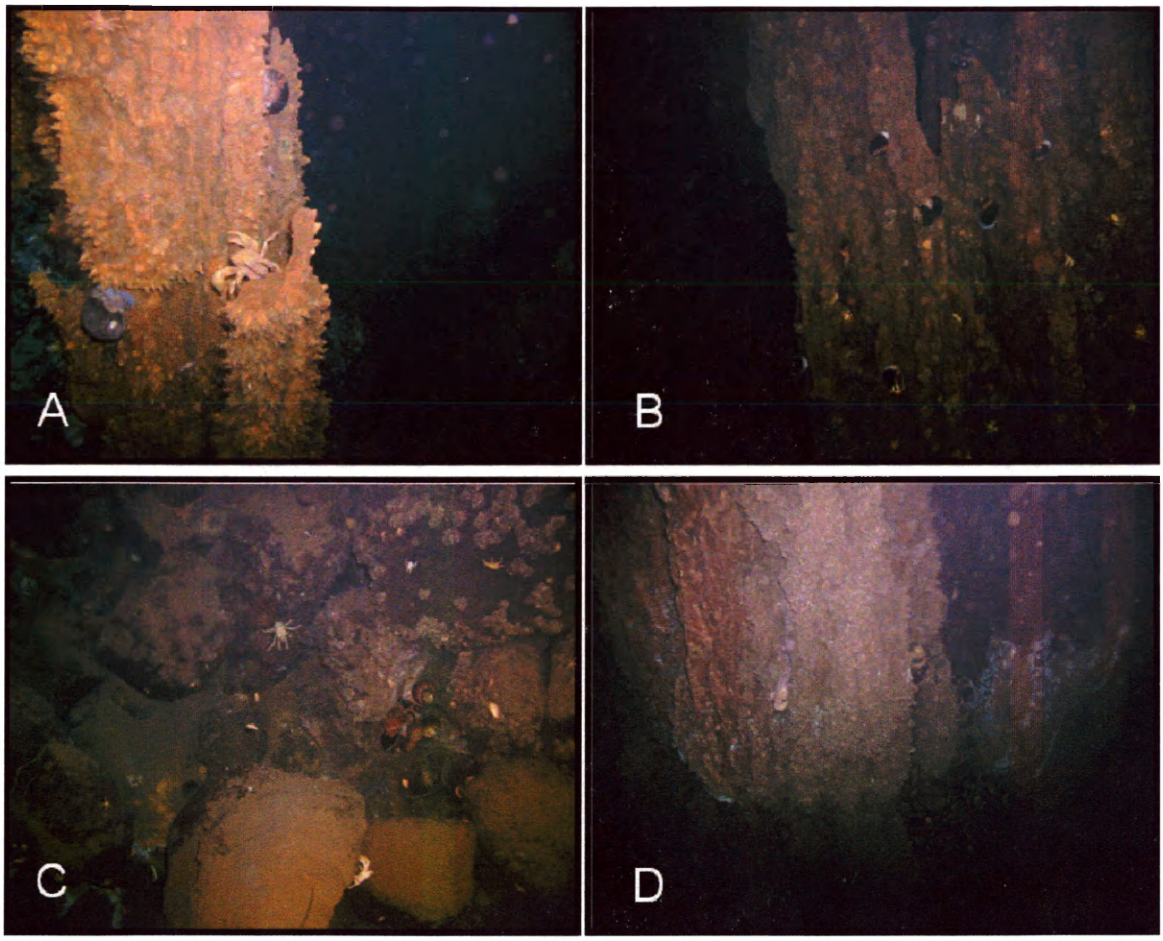


TABLE LEGENDS

Table 1. Site locations within the Suzette vent field and their dominant fauna.

Table 2. Macro- and megafauna observed at active hydrothermal vents and inactive sulfide mounds in the Suzette vent Field.

Table 3. Stable isotope composition (C, N, S) of active and inactive individual organisms from the Suzette vent field, Manus Basin.

Table 1. Site locations within the Suzette vent field and their dominant fauna

Site and habitats observed	Habitats sampled	Latitude (S)	Longitude (W)	Depth (m)	Inactive biomass dominant organisms	Active biomass dominant organisms
Williamson, AI	AI	-3.790589	152.0912824	1570	*Keratoisis* sp.	*Alvinoconcha* sp. 1, *Ifremeria nautilei*
Kowalczyk, AI	AI	-3.789491	152.0968758	1550	Stalked barnacles	*Alvinoconcha* sp. 1, *Ifremeria nautilei*
NatNat, AI	I	-3.789329	152.0977315	1560	*Keratoisis* sp.	*Alvinoconcha* sp. 1, *Ifremeria nautilei*
Fullagar Extended, AI	AI	-3.791047	152.0969462	1520	Hydroids, *Abyssocladia dominalba*	*Alvinoconcha* sp. 1, *Ifremeria nautilei*
Paine, AI	I	-3.788655	152.0935177	1500	Hydroids, *Munidopsis* spp.	*Alvinoconcha* sp. 1, *Ifremeria nautilei*
Binns, AI	AI	-3.788683	152.0943102	1500	Stalked barnacles, *Munidopsis* spp.	*Alvinoconcha* sp. 1, *Ifremeria nautilei*
Scott, AI	None	-3.789407	152.0926433	1520	Stalked barnacles, *Munidopsis* spp.	*Alvinoconcha* sp. 1, *Ifremeria nautilei*
Max, I	None	-3.789217	152.0934033	1600	*Keratoisis* sp.	Not applicable
99, I	I	-3.784692	152.0922521	1600	*Keratoisis* sp.	Not applicable
Tumora, AI	None	-3.789227	152.0922983	1515	Hydroids, orange bacterial mats	*Alvinoconcha* sp. 1, *Ifremeria nautilei*
Kambek *	None	-3.789532	152.0893267	1500	Not applicable	Not applicable

A - active habitat; I - inactive habitat; * no observations or transects were made at this location

Table 2. Macro- and megafauna observed and collected at active hydrothermal vents and inactive sulfide mounds in the Suzette vent Field. The symbol * represents organisms from inactive sample sites; The symbol • represents organisms from active and inactive sites; The symbol † represents organisms observed but not collected.

Taxon	Phylum	Family	Group	Species Description
Acryptolaria sp.*	Cnidaria	lafoeidae	hydroid	
Halecium n. sp. 1 *	Cnidaria	haleciidae	hydroid	
*Stegolaria geniculata**	Cnidaria	tiarannidae	hydroid	Allman, 1888
Sertularella n. sp.*	Cnidaria	sertulariidae	hydroid	
Zoanthid	Cnidaria	zoanthidae	zoanthid	
cf. *Hadalanthus*sp. *	Cnidaria	actinostolidae	anemone	
cf. *Tealidium* sp. OR cf. *Bathydactylus* sp.	Cnidaria	actinostolidae	anemone	
Actinauge sp.	Cnidaria	hormathiidae	anemone	
Actinosctyphia cf. *saginata* † *	Cnidaria	actinoscyphiidae	anemone	Stephenson, 1920
Keratoisis sp.*	Cnidaria	isididae	coral	
*Abyssocladia dominalba**	Porifera	cladorhizidae	sponge	Vacelet in press
*Cladorhiza abyssicola**	Porifera	cladorhizidae	sponge	G.O. Sars 1872
Hesiospina vestimentifera	Annelida	hesionidae	polychaete	Blake 1985
Archinome rosacea	Annelida	hesionidae	polychaete	Blake 1985
Nereidiae	Annelida	nereidiae	polychaete	
Branchinotogluma cf. *trifurcus*	Annelida	polynoidae	polychaete	Miura & Desbruyères 1995
Branchinotogluma cf. *segonzci*	Annelida	polynoidae	polychaete	Miura & Desbruyères 1995
Opisthotrochopodus cf. *segonzaci*	Annelida	polynoidae	polychaete	Miura & Desbruyères 1995
Thermopolynoe cf. *branchiata*	Annelida	polynoidae	polychaete	Miura 1994
Lepidonotopodus sp.	Annelida	polynoidae	polychaete	
Nicomache cf. *arwidssoni*	Annelida	maldanidae	polychaete	Blake 1985
Chaetopteridae†	Annelida	chaetopteridae	polychaete	
Paralvinella hessleri	Annelida	alvinellidae	polychaete	Desbruyères & Laubier 1989
Paralvinella fijiensis	Annelida	alvinellidae	polychaete	Desbruyères & Laubier 1993
Paralvinella cf. *unidentata*	Annelida	alvinellidae	polychaete	Desbruyères & Laubier 1993
Amphisamytha galapagensis	Annelida	ampharetidae	polychaete	Zotolli 1983
Lepetodrilus schrolli	Mollusca	lepetodrilidae	limpet	Beck 1993
Shinkailepas tufari	Mollusca	phenacolepadidae	limpet	Beck 1992
Olgasolaris tollmanni	Mollusca	phenacolepadidae	limpet	Beck 1992
Eosipho desbruyeresi	Mollusca	buccinidae	gastropod	Okutani et al. 1993
Alvinoconcha sp. 1	Mollusca	provannidae	gastropod	Mentioned in Kojima et al. 1999
Desbruyeresia n. sp.1	Mollusca	provannidae	gastropod	Waren & Bouchet 1993
Ifremeria nautilei	Mollusca	provannidae	gastropod	Bouchet & Waren 1991; Beck 1991
Provanna buccinoides	Mollusca	provannidae	gastropod	Waren & Bouchet 1993
Provanna n. gen. sp. 1	Mollusca	provannidae	gastropod	Waren & Bouchet 2001
Eochionelasmus ohtai cf. *manuensis*	Arthropoda	chionelasmatoidae	Barnacle	Galkin 1992
Neolepas cf. *zevinae**	Arthropoda	neolepadidae	Barnacle	Newman 1979
Vulcanolepas cf. *parensis* •	Arthropoda	Elepadidae	Barnacle	Southward 2005
Poecilasma cf. *kaempferi**	Arthropoda	poecilasmatidae	Barnacle	Darwin 1852
*Megalasma (Glyptelasma) sp.**	Arthropoda	poecilasmatidae	Barnacle	
Altiverruca sp.*	Arthropoda		Barnacle	
Neoverruca sp.*	Arthropoda	neoverrucidae	Barnacle	
Scalpellomorph n. sp. *	Arthropoda	scalpellmorphidae	Barnacle	
Chorocaris vandoverae•	Arthropoda	alvinocaridae	shrimp	Martin & Hessler 1990

Taxon	Phylum	Family	Group	Species Description
Lebbeus n. sp.*	Arthropoda		shrimp	
Asellota	Arthropoda	ischnomesidae	isopod	
Ventiella cf. *sulfuri*	Arthropoda	uristidae	amphipod	Barnard & Ingram 1990
Paralomis cf. *spinosissima*† *	Arthropoda	lithodidae	stone crab	Birstein and Vinogradow 1972
Munidopsis lauensis •	Arthropoda	galatheidae	squat lobster	Baba & Saint Laurent 1992
Munidopsis starmer •	Arthropoda	galatheidae	squat lobster	Baba & Saint Laurent 1992
Austinograea alaysae	Arthropoda	bythograeidae	crab	Guinot 1989
*Chiridota hydrothermica**	Echinodermata	chiridotidae	Holothurian	Smirnov et al. 2000
Enypneastes cf. *exemia*† *	Echinodermata	synaptidae	holothurian	Theel 1882
Ophiura sp.*	Echinodermata	ophiuroidae	brittle Star	
Ophiacantha sp.*	Echinodermata	ophiuroidae	brittle Star	
Pyrolycus cf. *manusanus*• †		zoarcidae	eelpout	Machida & Hashimoto 2001

Table 3. Carbon, nitrogen, and sulfur isotopic compositions (‰) of individual organisms from active and inactive sulfide mounds from the Suzette vent field, Manus Basin.

Site location	Habitat type observed	Habitat type sampled	Tissue type	Organism	Feeding type	Carbon	Nitrogen	Sulfur
Fullagar	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-24.2	4.4	-0.1
Fullagar	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-26.8	4.9	-2.0
Fullagar	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-27.3	4.1	6.2
Fullagar	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-25.5	5.0	5.0
Fullagar	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-27.1	3.7	5.3
Binns	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-23.2	4.6	1.3
Binns	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-26.9	6.2	-2.9
Binns	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-28.0	6.5	-1.3
Binns	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-29.7	6.6	1.5
Binns	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-24.1	5.2	1.5
Binns	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-25.1	4.9	-2.0
Binns	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-24.7	4.6	1.2
Binns	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-24.9	3.7	-1.0
Williamson	A, I	Active	Muscle foot	*Alvinoconcha* sp. 1	Endosymbionts	-26.9	6.7	-9.4
Binns	A, I	Active	Muscle	*Austinagrae alaysea*	Scavenger	-20.1	8.4	-1.1
Binns	A, I	Active	Muscle	*Austinagrae alaysea*	Scavenger	-20.4	7.6	-0.6
Kowalczyk	A, I	Active	Muscle	*Austinagrae alaysea*	Scavenger	-19.8	8.5	-1.6
Binns	A, I	Active	Muscle	*Austinogreae alaysea*	Scavenger	-21.4	9.3	0.1
Binns	A, I	Active	Muscle	*Austinogreae alaysea*	Scavenger	-20.2	9.4	-5.3
Binns	A, I	Active	Muscle	*Austinogreae alaysea*	Scavenger	-20.7	8.9	-2.5
Binns	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-19.9	12.0	5.4
Williamson	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-21.8	9.6	3.3
Williamson	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-22.3	11.3	8.9
Williamson	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-23.5	9.6	7.9
Williamson	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-20.9	9.5	-1.5
Williamson	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-20.6	7.1	-0.5
Williamson	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-21.0	8.7	-0.1
Williamson	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-21.2	9.4	-1.8
Williamson	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-24.0	7.5	-6.6
Kowalczyk	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-	-	-4.1
Kowalczyk	A, I	Active	Abdomen	*Chorocaris vandoverae*	Scavenger	-23.0	7.0	-0.7
Fullagar	A, I	Active	Whole body	*Eochionelasmus ohtai* cf. *manuensis*	Suspension	-26.3	8.2	2.1
Fullagar	A, I	Active	Whole body	*Eochionelasmus ohtai* cf. *manuensis*	Suspension	-25.5	9.8	-1.7
Fullagar	A, I	Active	Whole body	*Eochionelasmus ohtai* cf. *manuensis*	Suspension	-26.0	8.9	-4.8

Site location	Habitat type observed	Habitat type sampled	Tissue type	Organism	Feeding type	Carbon	Nitrogen	Sulfur
Fullagar	A, I	Active	Whole body	*Eochionelasmus ohtai* cf. *manuensis*	Suspension	-21.9	10.2	3.0
Binns	A, I	Active	Whole body	*Eochionelasmus ohtai* cf. *manuensis*	Suspension	-21.0	5.4	1.2
Binns	A, I	Active	Whole body	*Eochionelasmus ohtai* cf. *manuensis*	Suspension	-26.8	6.0	1.1
Binns	A, I	Active	Whole body	*Eochionelasmus ohtai* cf. *manuensis*	Suspension	-25.2	7.6	-2.9
Williamson	A, I	Active	Muscle foot	*Eosipho sp.*	Predator	-28.3	9.1	-7.3
Binns	A, I	Active	Whole	*Acryptolaria/Halecium/Stegolaria/ Sertularella* Δ	Suspension	-21.8	8.3	-
Fullagar	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-26.9	4.9	6.1
Fullagar	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-25.0	5.0	4.7
Fullagar	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-24.8	3.8	4.8
Fullagar	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-25.5	6.2	1.5
Binns	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-26.8	4.2	2.3
Binns	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-27.0	3.1	-6.3
Williamson	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-25.8	6.9	3.8
Williamson	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-26.9	5.5	3.3
Binns	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-22.8	6.9	4.1
Kowalczyk	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-26.9	4.0	-2.4
Binns	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-23.8	1.0	-3.8
Binns	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-24.9	1.9	-0.4
Binns	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-26.6	2.5	1.1
Binns	A, I	Active	Muscle foot	*Ifremeria nautilei*	Endosymbionts	-27.2	3.1	5.4
Fullagar	A, I	Active	Whole specimens pooled	*Lepetodrilus/Olgasolaris* Δ	Grazer	-21.6	4.3	6.1
Binns	A, I	Active	Whole specimens pooled	*Lepetodrilus/Olgasolaris* Δ	Grazer	-22.4	2.9	3.2
Binns	A, I	Active	Whole specimens pooled	*Lepetodrilus/Olgasolaris* Δ	Grazer	-21.9	5.9	0.4
Binns	A, I	Active	Whole specimens pooled	*Lepetodrilus/Olgasolaris* Δ	Grazer	-22.4	3.8	-2.6
Binns	A, I	Active	Whole specimens pooled	*Lepetodrilus/Olgasolaris* Δ	Grazer	-20.9	6.3	4.7
Kowalczyk	A, I	Active	Whole specimens pooled	*Lepetodrilus/Olgasolaris* Δ	Grazer	-21.6	5.9	1.2
Kowalczyk	A, I	Active	Abdomen	*Munidopsis lauensis*	Scavenger	-22.4	6.2	1.2
Williamson	A, I	Active	Whole specimer	*Volcanolepas* cf. *parensis*	Suspension	-22.0	11.9	-
Binns	A, I	Inactive	Whole specimer	*Abyssocladia domnalba*	Predator	-21.0	9.9	0.5
Williamson	A, I	Inactive	Sponge top	*Abyssocladia domnalba*	Predator	-18.8	14.0	-3.2
Williamson	A, I	Inactive	Sponge top	*Abyssocladia domnalba*	Predator	-20.4	14.0	-2.0
Williamson	A, I	Inactive	Sponge top	*Abyssocladia domnalba*	Predator	-19.8	12.0	-3.0
Williamson	A, I	Inactive	Sponge top	*Abyssocladia domnalba*	Predator	-20.9	11.9	-2.9
Paine	A, I	Inactive	Sponge top	*Abyssocladia domnalba*	Predator	-18.8	12.0	-0.7
NatNat	A, I	Inactive	Sponge top	*Abyssocladia domnalba*	Predator	-18.9	10.8	2.5

Site location	Habitat type observed	Habitat type sampled	Tissue type	Organism	Feeding type	Carbon	Nitrogen	Sulfur
Fullagar	A, I	Inactive	Whole specimen	Asellota	Scavenger	-22.2	12.5	-
Fullagar	A, I	Inactive	Body wall	*Chiridota hydrothermica*	Depcsit	-22.6	5.5	5.1
Fullagar	A, I	Inactive	Intestine	*Chiridota hydrothermica*	Depcsit	-25.8	3.1	4.3
NatNat	A, I	Inactive	Whole specimen	*Chiedorhiza abyssicola*	Predator	-18.3	12.0	1.7
Binns	A, I	Inactive	Abdomen	*Chorocaris vandoverae*	Scavenger	-22.2	8.8	-1.8
Binns	A, I	Inactive	Abdomen	*Chorocaris vandoverae*	Scavenger	-21.1	9.8	6.3
Binns	A, I	Inactive	Whole	*Acryptolaria/Halecium/Stegolaria/Sertularella* Δ	Suspension	-21.2	8.9	4.2
Williamson	A, I	Inactive	Whole	*Acryptolaria/Halecium/Stegolaria/Sertularella* Δ	Suspension	-21.7	8.2	-9.9
Paine	A, I	Inactive	Whole	*Acryptolaria/Halecium/Stegolaria/Sertularella* Δ	Suspension	-	-	-8.0
99	I	Inactive	Whole	*Acryptolaria/Halecium/Stegolaria/Sertularella* Δ	Suspension	-22.4	9.4	-4.8
Fullagar	A, I	Inactive	Whole	*Acryptolaria/Halecium/Stegolaria/Sertularella* Δ	Suspension	-5.6	8.6	-
Williamson	A, I	Inactive	Whole specimen	cf. *Hadalanthus* sp.	Suspension	-20.0	11.4	-9.0
Williamson	A, I	Inactive	Whole specimen	cf. *Hadalanthus* sp.	Suspension	-19.2	11.6	-9.0
99	I	Inactive	Whole specimen	cf. *Hadalanthus* sp.	Suspension	-19.2	16.9	-3.6
Williamson	A, I	Inactive	Skeleton and polyps	*Keratoisis sp.*	Suspension	-20.1	12.1	-9.2
Williamson	A, I	Inactive	Skeleton and polyps	*Keratoisis sp.*	Suspension	-21.0	11.8	-9.8
Williamson	A, I	Inactive	Skeleton and polyps	*Keratoisis sp.*	Suspension	-18.6	11.7	-7.6
Williamson	A, I	Inactive	Skeleton and polyps	*Keratoisis sp.*	Suspension	-21.2	13.0	-6.5
99	I	Inactive	Cuticle	*Keratoisis sp.*	Suspension	-21.9	12.7	-3.1
99	I	Inactive	Cuticle	*Keratoisis sp.*	Suspension	-20.2	12.4	-1.7
Binns	A, I	Inactive	Abdomen	*Munidopsis lauensis or starmer* Δ	Scavenger	-21.9	5.9	5.3
Binns	A, I	Inactive	Abdomen	*Munidopsis lauensis or starmer* Δ	Scavenger	-21.8	4.5	3.8
Binns	A, I	Inactive	Abdomen	*Munidopsis lauensis or starmer* Δ	Scavenger	-22.0	6.0	3.7
Binns	A, I	Inactive	Abdomen	*Munidopsis lauensis or starmer* Δ	Scavenger	-22.7	5.8	1.2
Williamson	A, I	Inactive	Abdomen	*Munidopsis lauensis or starmer* Δ	Scavenger	-17.2	7.0	-9.0
Paine	A, I	Inactive	Abdomen	*Munidopsis lauensis or starmer* Δ	Scavenger	-21.8	6.4	3.7
Fullagar	A, I	Inactive	Abdomen	*Munidopsis lauensis or starmer* Δ	Scavenger	-21.2	6.2	2.4
99	I	Inactive	Gonads	*Ophiacantha* sp.	Depcsit	-22.3	11.1	-5.5
Fullagar	A, I	Inactive	Whole specimen	*Ventiella cf. sulfuris*	Scavenger	-23.7	1.4	-
Binns	A, I	Inactive	Whole body	*Volcanolepas* cf. *parensis*	Suspension	-20.0	12.4	-1.8
Binns	A, I	Inactive	Whole body	*Volcanolepas* cf. *parensis*	Suspension	-21.2	10.0	5.8
99	I	Inactive	Whole body	*Volcanolepas* cf. *parensis*	Suspension	-22.9	8.7	-6.6
Fullagar	A, I	Inactive	Whole body	*Volcanolepas* cf. *parensis*	Suspension	-22.3	12.0	3.0
Fullagar	A, I	Active	Substrate samples					1.1
Binns	A, I	Active	Substrate samples					-2.6
Williamson	A, I	Active	Substrate samples					-2.2

Site location	Habitat type observed	Habitat type sampled	Tissue type	Organism	Feeding type	Carbon	Nitrogen	Sulfur
Binns	A, I	Active	Substrate samples					-2.0
Kowalczyk	A, I	Active	Substrate samples					
Fullagar	A, I	Inactive	Substrate samples					-0.6
Binns	A, I	Inactive	Substrate samples					-3.4
Williamson	A, I	Inactive	Substrate samples					1.7
Williamson	A, I	Inactive	Substrate samples					-1.9
99		Inactive	Substrate samples					-1.2
Paine	A, I	Inactive	Substrate samples					3.8
Nat Nat	A, I	Inactive	Substrate samples					2.6
Kowalczyk	A, I	Inactive	Substrate samples			-	-	3.3

Δ not identified to species, * replicate samples were averaged, - sample lost or too small

APPENDIX A

Macro- and megafauna observed and collected from active hydrothermal chimneys and inactive sulfide mounds in the Suzette vent field, Manus Basin, Papua New Guinea

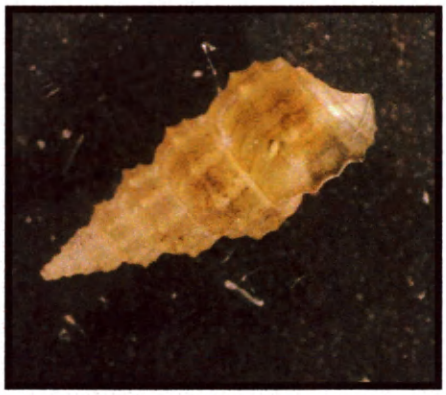
A field guide for taxonomic identification

Suzette vent field:
Invertebrates from active hydrothermal chimney

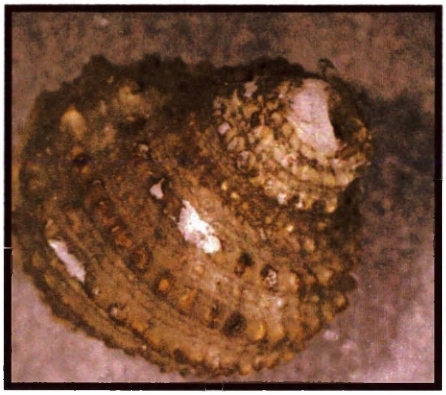
Lepetodrilus schrolli

Olgasolaris tollmanni

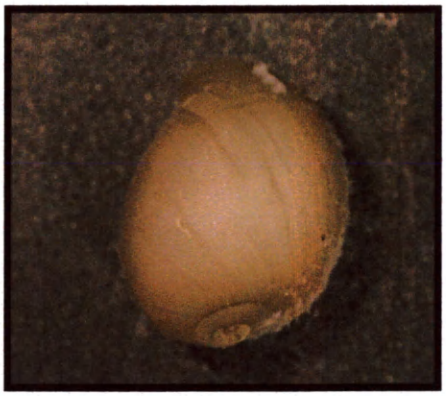
Provanna n. gen. sp.1



Desbruyeresia n. sp.1



Ifremeria nautilei (Immature)

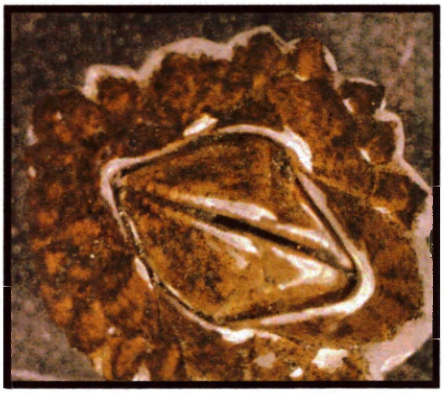


Alvinoconcha sp. 1 (Immature)

Ifremeria nautilei

Alvinoconcha sp. *1*

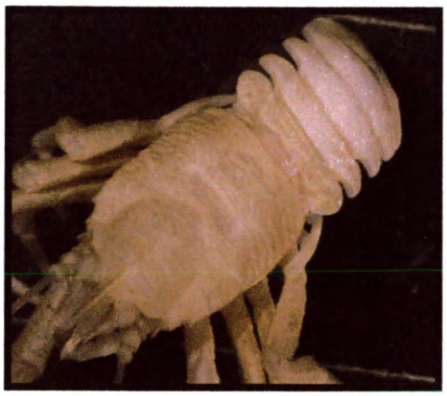
Eosipho desbruyeresi



Eochionelasmus ohtai cf. *manusensis*

Austinograea alaysae

cf. *Tealidium* or *Bathydactylus*



Munidopsis lauensis

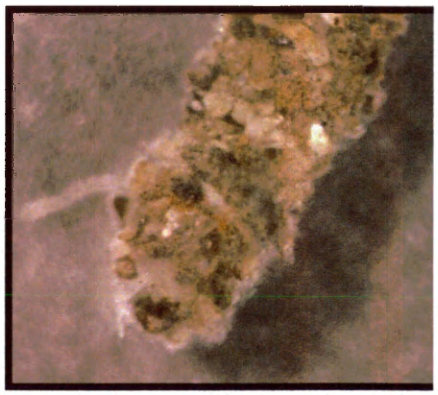
Sabellidae (tubes)

Chorocaris vandoverae

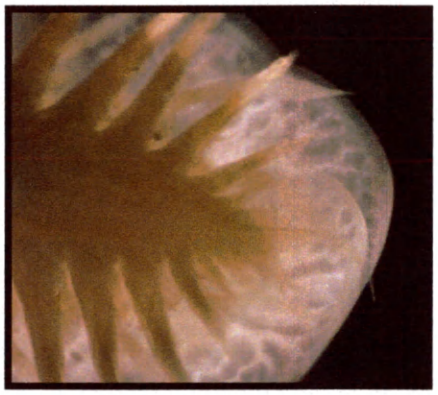
Archinome rosacea

Shinkailepas tufari

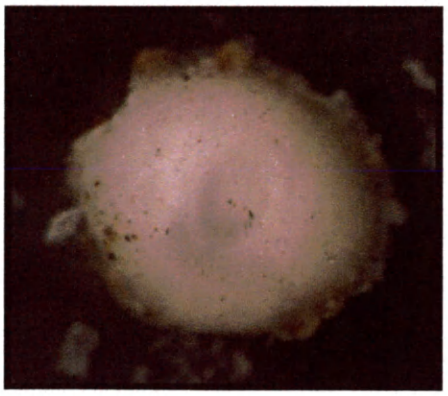
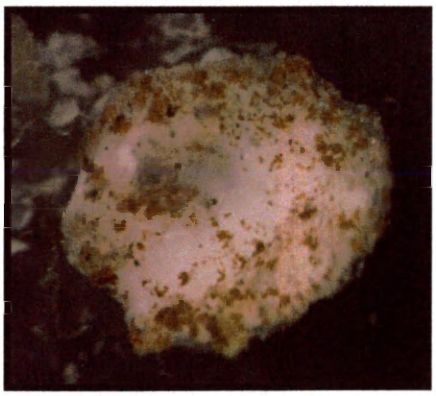
Paralvinella hessleri

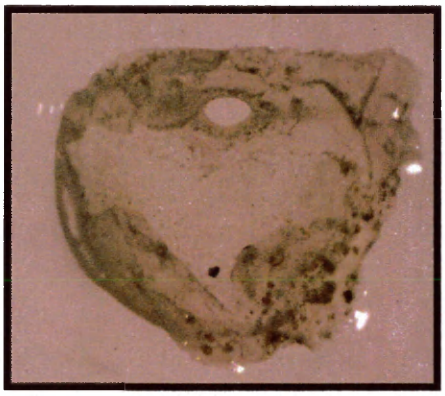
Amphisamytha galapagensis

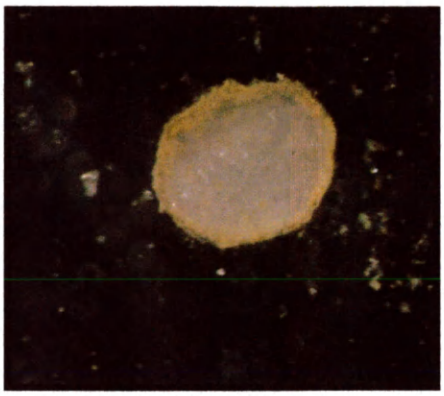
Branchinotogluma cf. *trifurcus*

Turridae egg capsule

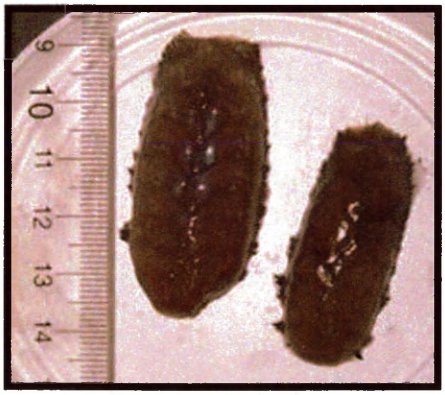


Turridae egg capsule (empty)



Turridae egg capsule

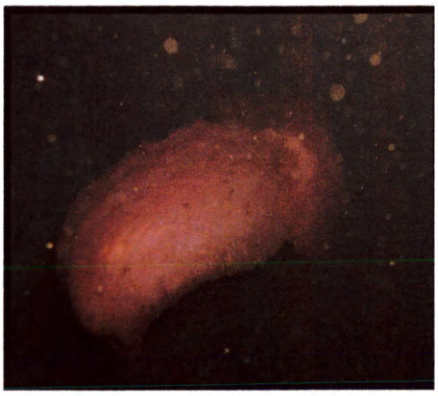
Thermopolynoe cf. *branchiata*



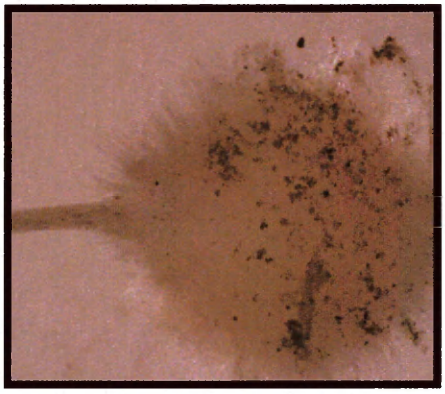
Branchinotogluma cf. *segonzci*

Suzette vent field:
Invertebrates from inactive sulfide mounds

Actinosctyphia cf. *saginata*

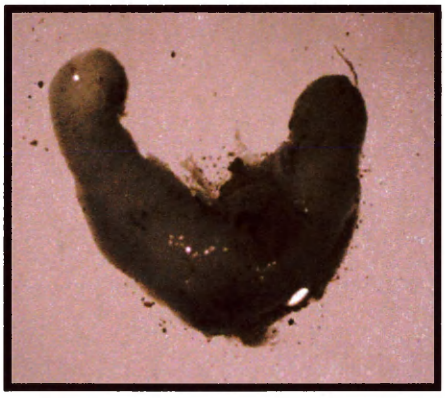


Enypniastes cf. *eximia*



Abyssocladia dominalba

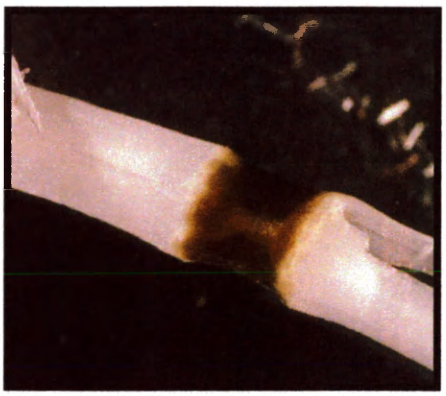
Actinauge sp.



Aplacophoran

cf. *Hadalanthus* sp.

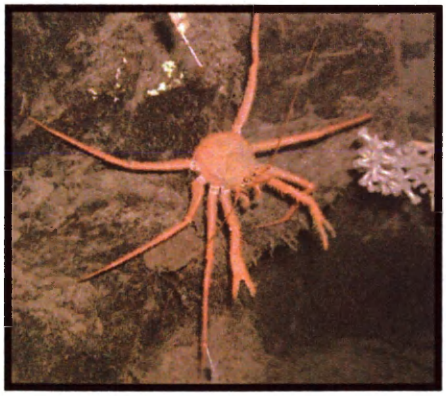
Keratoisis sp.



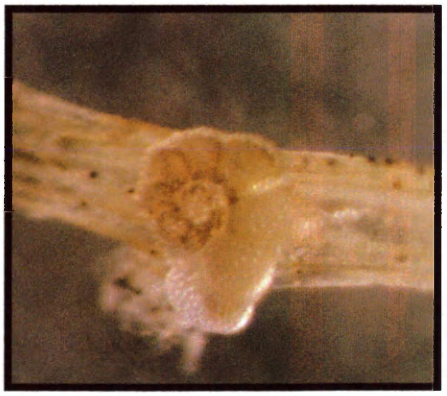
Keratoisis sp. skeleton

Keratoisis sp. (polyps)

Keratoisis sp.

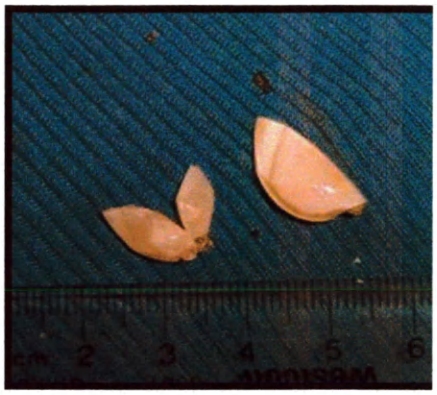


Paralomis cf. *spinosissima*



Foraminifera

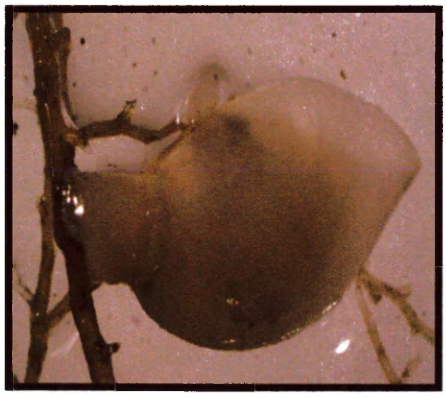
Vulcanolepas cf. *parensis*



Poecilasma cf. kaempferi

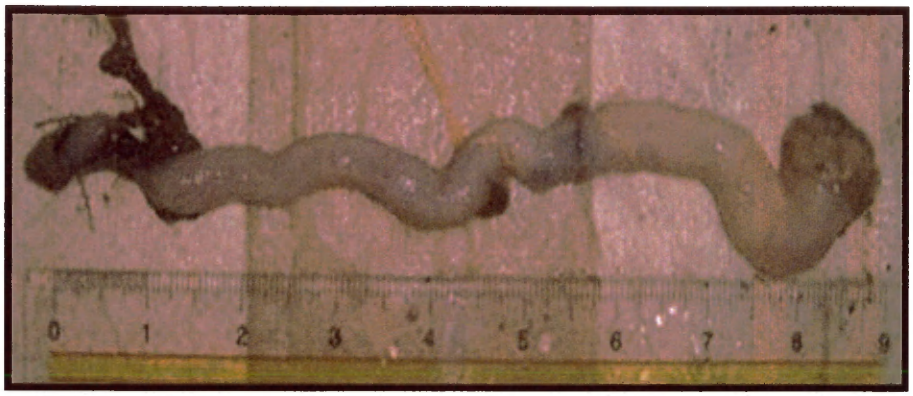
Neolapas cf. zevinae

Altiverruca sp.

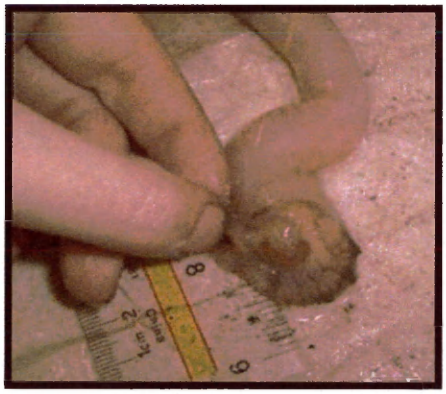


Megalasma (Glyptelasma)

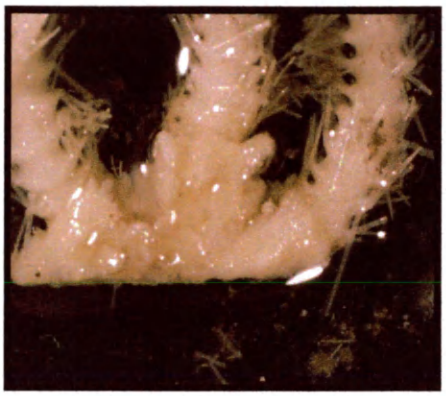
Scalpellomorph



Chiridota hydrothermica



Lebbeus sp.



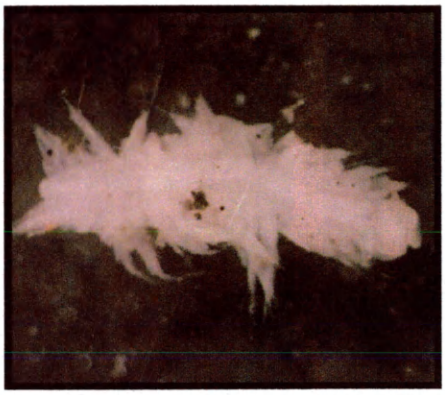
Ophiacantha sp.

Ophiura sp.

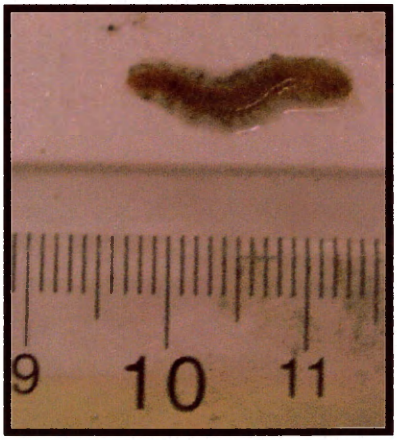
Asellota (isopod)

Ventiella cf. sulfuris

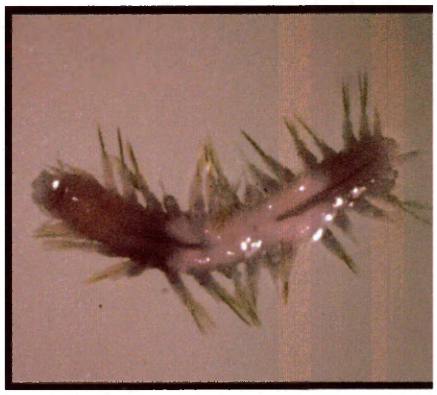
Cladorhiza abyssocola



Polychaete from
Cladorhiza abyssocola



Nereis cf. *sandersi*



Hesionidae

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